
A TAXONOMIC REVISION OF THE GENUS *PHYLA* (VERBENACEAE)¹

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ABSTRACT

A taxonomic revision of the genus *Phyla* Lour. is provided. *Phyla* is a small genus in Verbenaceae, placed in the tribe Lantaneae and represented by five species and three varieties. Four species are found only in the Americas, and one, *P. nodiflora* (L.) Greene, is found worldwide in tropical and temperate areas. Detailed morphological descriptions are given for each taxon, as well as a key for their identification, illustrations, synonymy, distribution, selected specimens, and discussion about the relationships among closely related taxa. *Cryptocalyx nepetifolia* Benth. is lectotypified, and one new combination is proposed, *P. nodiflora* var. *minor* (Hook.) N. O'Leary & Múlgura.

Key words: Americas, *Lippia*, *Phyla*, taxonomy, Verbenaceae.

Loureiro (1790) founded *Phyla* Lour. with a species from Cochinchina, Vietnam, which he named *P. chinensis* Lour. (a synonym of *P. nodiflora* (L.) Greene). *Phyla* belongs to tribe Lantaneae (Schauer) Briq., along with the closely related genera *Lippia* L., *Lantana* L., *Aloysia* Paláu, and others (Atkins, 2004). Many botanists have treated *Phyla* under *Lippia* (Schauer, 1847; Briquet, 1895; Macbride, 1960; Gibson, 1970; Jansen-Jacobs, 1988; Brako & Zarucchi, 1993; Sanders, 2001; Rzedowski & Rzedowski, 2002). However, both genera have been accepted as distinct by various authors (Greene, 1899; Moldenke, 1942, 1973a, 1983; Troncoso, 1965, 1979; Wiggins & Porter, 1971; López-Palacios, 1977; Wiggins, 1980; Munir, 1993; Troncoso & Botta, 1993; Jørgensen & León-Yáñez, 1999; Pool, 2001; Méndez Santos, 2003; Múlgura, 2003; Atkins, 2004).

In the following treatment, five species under *Phyla* are recognized, with three infraspecific taxa for *P. nodiflora*. *Phyla*, with its prostrate herbaceous plants rooting at the nodes, malpighiaceae hairs, and generally uncinata hairs on the calyx, is distinguished from the closely related genus *Lippia*. In contrast, *Lippia* is defined as a taxon of spreading shrubs, with simple, non-malpighiaceae hairs and the absence of uncinata hairs on the calyx (Greene, 1899). In addition, phylogenetic studies (Marx et al., 2010) show *Phyla*, as circumscribed here, as a highly supported monophyletic group.

MATERIALS AND METHODS

This taxonomic revision is based on herbarium collections from the following herbaria: BM, G, MO, NY, SI, and US. Flower measurements were taken from material rehydrated by boiling. Fruit measurements were taken from dried specimens. The descriptive terminology of the inflorescences used here is in accordance with Múlgura et al. (2002), the morphological terms follow Hickey (1974), and the description of pubescence corresponds to Lawrence (1951). We considered varietal status for taxa when we observed a group of organisms with a gradual variation of characters, which would suggest an incomplete segregation of two incipient species sharing the same geographical area, following Suttill and Allen (1992), who considered varieties when differences were morphological but not geographical. The distribution and habitat data of taxa were taken from herbarium specimen labels. Appendix 1 includes a list of accepted taxa and a complete list of examined specimens.

TAXONOMIC TREATMENT

I. *Phyla* Lour., Fl. Cochinch. 66. 1790. *Piarimula* Raf., Fl. Tellur. 2: 102. 1836, nom. illeg. TYPE: *Phyla chinensis* Lour. [= *Phyla nodiflora* (L.) Greene].

Pilopus Raf., Fl. Tellur. 2: 102. 1836 [1837], replacement name for *Bertolonia* Raf., *Chloris* Aetn. 5. 1815, nom.

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illeg., non *Bertolonia* Spin, 1809. TYPE: *Pilopus nodiflora* Raf. [= *Phyla nodiflora* (L.) Greene].
Diototheca Raf., Fl. Ludov. 74. 1817. TYPE: *Diototheca repens* Raf. [= *Phyla nodiflora* (L.) Greene].
Cryptocalyx Benth., Ann. Nat. Hist., 2(12): 446. 1839. TYPE: *Cryptocalyx nepetifolia* Benth. [= *Phyla betulifolia* (Kunth) Greene].

Perennial, usually procumbent *herbs*, stems sometimes basally slightly woody, often rooting at nodes, usually densely covered with adpressed strigose, mostly malpighian (medifixed) acute hairs, rarely subglabrous. *Leaves* petiolate or subsessile; simple, decussate-opposite, margins entire or serrate-dentate. *Synflorescences* frondose, arranged in a homothetic pleiobotryum, the florescences solitary or to 3 per leaf axil, peduncled, spiciform or capitate and globose at anthesis, but later ovoid to oblong and cylindrical, densely flowered, with imbricate floral bracts. *Flowers* zygomorphic, perfect, sessile, small; floral bracts ovate to elliptic, apex often acute or acuminate, margin membranous; calyx persistent, membranous, compressed, keeled on each face, 2- to 4-dentate, subglabrous or pubescent with strigose, uncinata and glandular hairs; corolla hypocrateriform, tube straight or incurved, weakly exerted from calyx, mostly white, lavender to purple, limb 2-lipped, lobes broad or not; stamens 4, didynamous, included or sometimes slightly exerted, anthers not appendaged; ovary 1-carpellate, 2-locular, 1 ovule per locule, style terminal, stigma oblique. *Fruit* small, dry, obovoid to ellipsoid, included in the mature calyx and sometimes adnate to it, dividing at maturity into 2 nutlets, pericarp papraceous.

Distribution. *Phyla* is widely distributed, growing in temperate, tropical and subtropical North and South America, with the exception of *P. nodiflora*, which is found on every continent.

Chromosome number. Lewis (1961) studied chromosome numbers for several *Phyla* species—*P. lanceolata* (Michx.) Greene, *P. nodiflora*, and *P. nodiflora* var. *reptans* (Kunth) Moldenke (sub. nom. *P. strigulosa* (M. Martens & Galeotti) Moldenke)—and consistently reported a diploid number of $2n = 36$, suggesting that this chromosome number seemed to be frequent in the genus. Additional chromosome counts reported for the widespread taxon known as *P. nodiflora* have also been $2n = 36$ (Covas & Schnack, 1946; Sharma, 1970; Bir & Sidhu, 1980).

TAXONOMIC KEY TO SPECIES OF *PHYLA*

- 1a. Florescences 2 to 3 per axil; leaves with a petiole 1–2 cm long 1. *P. betulifolia*
- 1b. Florescences 1 per axil; leaves sessile or subsessile 2

- 2a. Leaves thick and coriaceous, margins entire or with 1 to 3 pairs of teeth 3
- 2b. Leaves chartaceous, margins entire, serrate or toothed 4
- 3a. Leaf blade oblong to obovate, 1–5 × 0.5–1 cm, base cuneate 2. *P. cuneifolia* (Torr.) Greene
- 3b. Leaf blade linear, 1.5–3 × 0.3–0.4 cm, base connate to the opposite leaf
..... 4. *P. linearis* (Kunth) Tronc. & López-Pal.
- 4a. Leaf blades elliptic; subglabrous with slightly adpressed strigose pubescence; plants restricted to the United States 3. *P. lanceolata*
- 4b. Leaf blades obovate, spatulate, or ovate to rhombic-ovate; subglabrous with slightly adpressed strigose pubescence; if blades elliptic then with canescent pubescence and white strigose hairs; plants distributed worldwide
..... 5. *P. nodiflora*

1. *Phyla betulifolia* (Kunth) Greene, Pittonia 4: 48. 1899. Basionym: *Lippia betulifolia* Kunth, Nov. Gen. Sp. [H.B.K.] (quarto ed.) 2: 264. 1818. TYPE: Venezuela. Apure: San Fernando, s.d., *F. W. Humboldt & A. Bonpland 1139* (holotype, P-604475 not seen, P-604475 photo at SI!; isotypes, B-W 11121-01 not seen, B-W 11121-01 photo at SI!, P-307284 not seen, P-307284 photo at SI!, P-307283 not seen, P-307283 photo at SI!, photo F neg. 39487!). Figure 1.

Cryptocalyx nepetifolia Benth., Ann. Nat. Hist. 2(12): 446. 1839. TYPE: British Guiana. Berbice, s.d., *R. Schomburgk 694* (lectotype, selected here, K not seen, K photo at SI!; duplicates of lectotype, BM not seen, BM photo at SI!; TCD not seen, TCD photo at SI!).

Perennial *herbs*, 15–60 cm, base woody, flowering stems erect, branches decumbent, rooting at nodes, generally with strigose and malpighiaceous hairs. *Leaves* with petioles 1–2 cm; blade ovate to nearly rhombic-ovate, 2–7(–9) × 1.5–5 cm, chartaceous or submembranous, venation prominent abaxially, slightly impressed adaxially; strigose pubescence and malpighiaceous hairs on both surfaces; base cuneate and decurrent, margins serrate from the widest part of the blade to the apex, the teeth mucronate, apex acute. *Florescences* ovoid to oblong spikes, 2 to 3 per axil, 1 × 0.3–0.5 cm at anthesis, elongating to 1.2 cm at maturity; short peduncles generally 0.5–0.8 cm, not surpassing leaves, flowers forming vertical lines in the spike; *floral bracts* elliptic, 2–3 mm, abruptly contracted to acuminate apex 0.8–1.5 mm, strigose hairs along margins and malpighiaceous hairs on abaxial surface, glabrous adaxially; *calyx* 0.8 mm, lobed to not more than half the length of the calyx, membranous with thickened lateral edges, margins with short scattered glandular hairs and short strigose hairs; *corolla* generally white,

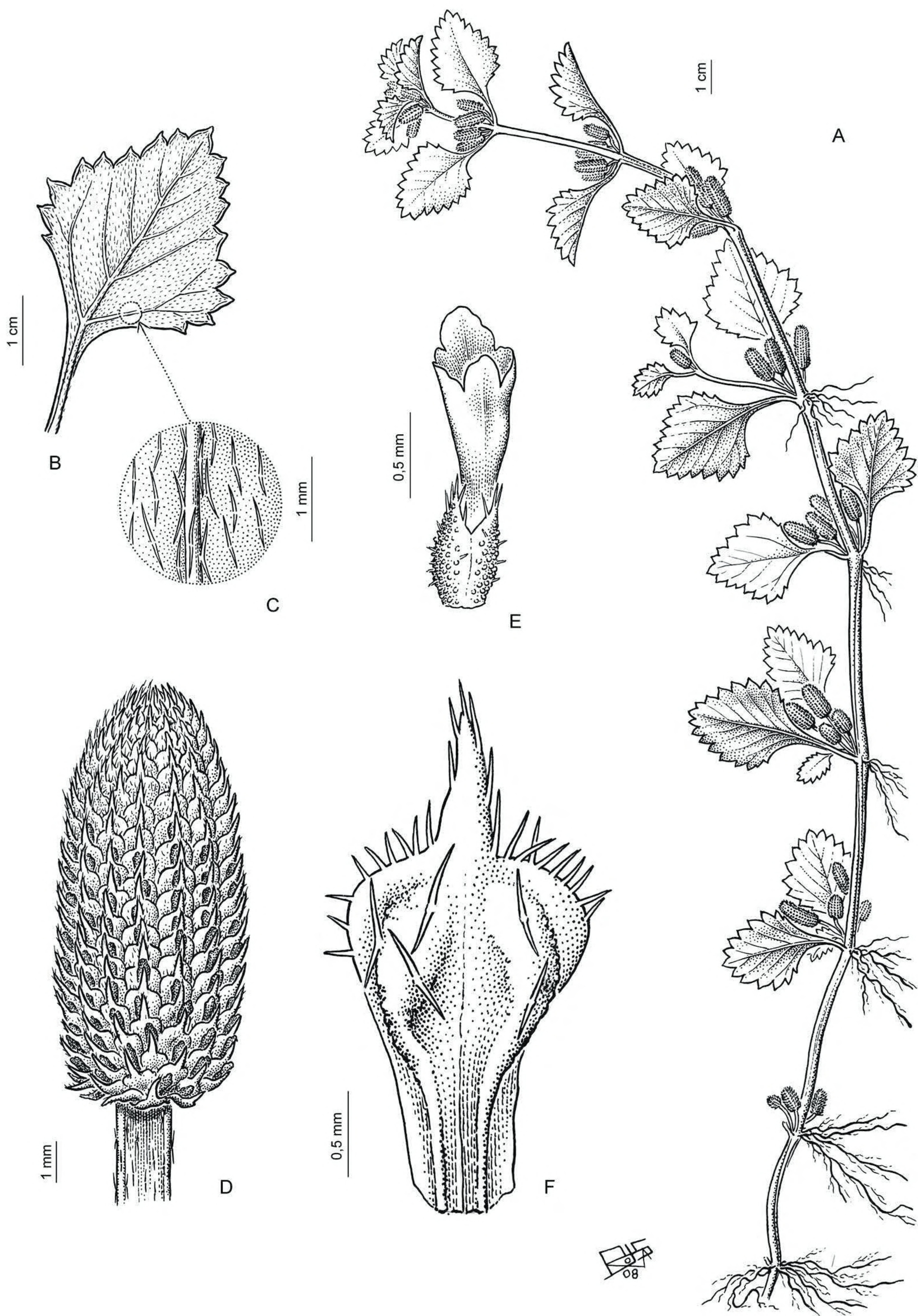


Figure 1. *Phyla betulifolia* (Kunth) Greene. —A. General aspect of plant. —B. Abaxial leaf surface. —C. Detail of pubescence of abaxial leaf surface. —D. Detail of florescence. —E. Flower. —F. Floral bract. A–C from *Rojas 2523* (SI); D, F from *Rojas 1884* (SI).

pale pink or pale purple, 1.8–2 mm, glabrous inside and outside except a narrow band of short hairs at the base of the lobes, lobes brief, erect, not conspicuous. *Fruit* dry, brown to yellow, each cluse 1 mm, obovoid, apex elongate.

Distribution and habitat. Collections of *Phyla betulifolia* have been made from Costa Rica, Guatemala, Honduras, and Panama in Central America, from Cuba and Trinidad in the West Indies, and from Bolivia, Brazil, Colombia, Ecuador, Paraguay, and Venezuela in tropical South America. It grows in low grounds, riverbanks and open woods, savannas, pastures and ruderal places, and is often found in sandy or clay soil.

Phenology. In Central America, *Phyla betulifolia* flowers principally between February and July and in South America mostly between July and November, so it can be found flowering in all seasons across this range.

Taxonomic notes. This species is easily recognized by its leaves that are ovoid to almost rhombic, with distinct petioles, and also by the presence of two or three shortly peduncled florescences at each leaf axil, floral bracts with conspicuous apices (cf. Fig. 1F), and minute flowers. All other species of *Phyla* have solitary florescences in leaf axils and leaves that are sessile or subsessile and never petiolate.

In his protologue for *Cryptocalyx nepetifolia*, Bentham cited two collections: *Gardner 1049* (G not seen, G photo SI!, S not seen, S photo SI!, US not seen, US photo SI!) and *Schomburgk 694* (BM not seen, BM photo SI!, K not seen, K photo SI!). Thus, a lectotype is designated, with *Schomburgk 694* at Kew chosen because it is a complete and well-preserved specimen. Bentham (1839) states that *Cryptocalyx* differs from *Lippia* by its tenuous calyx, its small corolla limb, the complete separation of the fruit, and its capituliform florescences. Our analyses of the type material support that Bentham's concept of *Cryptocalyx* refers to *Phyla*.

Selected specimens examined. CUBA. **Oriente [Granma]:** Manzanillo, Sabana del Mar, *Ekman 5645* (US). **Pinar del Río:** San Cristóbal, *Ekman 13750* (US). COSTA RICA. **Alajuela:** San Carlos, Los Chiles, *Zamora 1404* (MO). EL SALVADOR. **Ahuachapán:** Santa Rita, *Rosales 2216* (MO). GUATEMALA. **Izabal:** Quirigua, *Standley 23865* (US). HONDURAS. **Atlántida:** La Fragua, *Standley 55685* (US). NICARAGUA. **Río San Juan:** San Carlos, *Seymour 5351* (MO). **Zelaya:** Bonanza through Constancia, *Stevens 8026* (MO). PANAMA. **Panamá:** La Jagua, *Bartlett 16371* (MO). TRINIDAD. St. Augustine lands, Imperial College of Tropical Agriculture, *Broadway 7206* (MO, US). BOLIVIA. **Pando:** Madre de Dios, *Beck 20455* (SI). BRAZIL. **Acre:** Tarauacá, *Prance 7347* (MO). **Amazonas:** Ilha das Oncas,

Mexia 6068 (MO, US). **Bahia:** Livramento do Brumado, lagoa da Jurema, *Harley 25868* (MO). **Pernambuco:** Recife, *Vasconcellos Sobinho 4099* (US); s. loc., *Gardner 1049* (syntype of *Cryptocalyx nepetifolia*, G, S, US). **Rondônia:** Porto Velho, *Duarte 7317* (SI). COLOMBIA. **Amazonas:** Río Loretoyacu, *Evans Schultes 6597* (US). **Antioquia:** Puerto Berrio, *Archer 1402* (US). **Bolívar:** San Martín de Loba, El Garcelero, *Ramirez Arango 4597* (MO). **Boyacá:** Los Llanos, *Haught 2825* (US). **Santander:** Boca Sogamoso, río Magdalena, *Pennell 3840* (US). ECUADOR. **Guayas:** Balao, *Eggers 14275* (US). GUYANA. **Demerara-Mahaica:** Jct. Sheriff St. & David St., *Hill 27103* (US). **Pomeroon-Supenaam:** Lama Guest House, *Dowell 4172* (US). **Upper Takutu-Upper Essequibo:** Rewa River, *Clarke 3861* (US). PARAGUAY. **Alto Paraguay:** Itapucumí, playas río Paraguay, *Rojas 2523* (SI); Paraguay septentrionalis, *Hassler 7553* (BM). **Concepción:** Itacurubí, río Paraguay, *T. Rojas 1884* (SI). PERU. **Loreto:** Iquitos, río Itaya, *R. Scolnik 1164* (SI). **Tumbes:** Rivera izquierda río Tumbes, *López & Sagástegui 4024* (SI). **Ucayali:** Coronel Portillo, Yaracocha, *Graham 363* (MO). VENEZUELA. **Amazonas:** Río Negro, río Casiquiare, *Stergios 8135* (MO). **Apure:** Puerto Piez, *Velez 2242* (US). **Carabobo:** Valencia, *Saer 827* (US). **Cojedes:** betw. S. Carlos & S. Rafael, *Pittier 11722* (US). **Delta Amacuro:** Paloma, *Rusby 6* (US). **Guárico:** orillas río Manati, 4 Dec. 1923, *Mayuel Grisol s.n.* (SI). **Monagas:** Boca de Uracoa, *Tamayo 3525* (SI). **Portuguesa:** Río Guanare & río Tucupido, *Liesner 12409* (MO).

2. *Phyla cuneifolia* (Torr.) Greene, Pittonia 4: 47. 1899. Basionym: *Zapania cuneifolia* Torr., Ann. Lyceum Nat. Hist. New York 2: 234. 1828. *Lippia cuneifolia* (Torr.) Steud., Nom. Bot. [Steudel], ed. 2, 2: 54. 1841. TYPE: U.S.A. Nebraska: "on the Platte," June 1820, *James s.n.* (holotype, NY not seen, NY photo at SI!). Figure 2.

Perennial *herbs*, 10–20(–30) cm, base woody, flowering stems sometimes ascending, branches decumbent, rooting at the nodes, generally conspicuously canescent with white strigose and malpighiaceus hairs. *Leaves* sessile; clustering in axils; blade oblong to obovate, 1–5 × 0.5–1 cm, thick and coriaceous, midvein prominent abaxially, slightly impressed adaxially; canescent pubescence of strigose and malpighiaceus hairs on both surfaces; base cuneate, margins entire or with 2 to 3 pairs of acute shallow teeth, apex acute. *Florescences* ovoid to oblong spikes, 1 per axil, 1 × 1 cm at anthesis, elongating to 2 cm at maturity; peduncles briefly surpassing leaves, generally 1–5 cm; *floral bracts* ovate, 3–5 mm, acute apex, adpressed canescent pubescence with malpighiaceus hairs on abaxial surface, glabrous adaxially; *calyx* 2.5 mm, lobed to not more than half the length of the calyx, membranous with thickened lateral edges, margins densely uncinat; *corolla* purple or white, 3–5 mm, glabrous inside and outside except a narrow band of

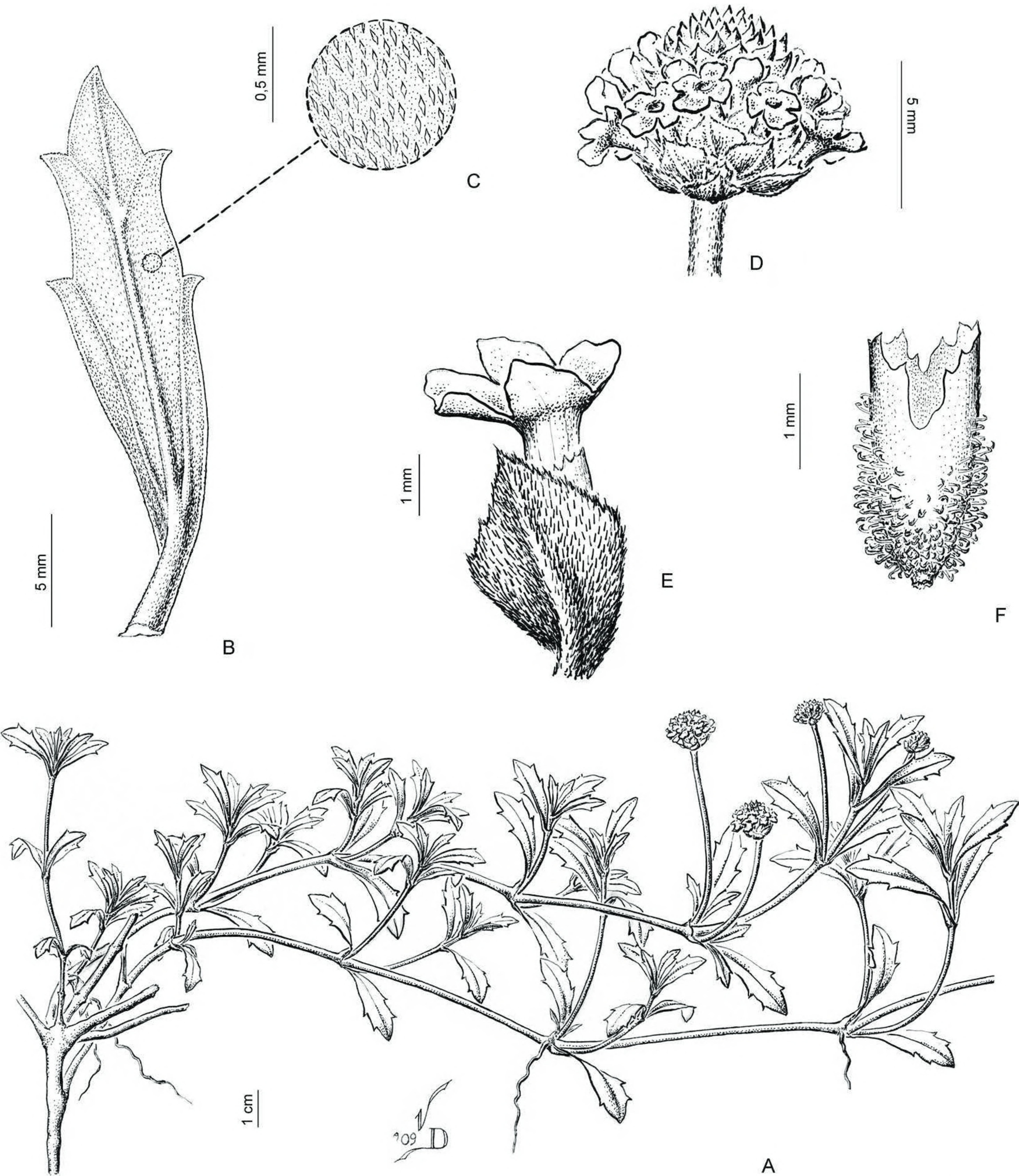


Figure 2. *Phyla cuneifolia* (Torr.) Greene. —A. General aspect of plant. —B. Abaxial leaf surface. —C. Detail of pubescence of abaxial leaf surface. —D. Detail of florescence. —E. Flower with floral bract. —F. Calyx. Drawn from *Crandall s.n.* (MO).

short hairs at the base of the developed lobes. *Fruit* dry, brown to yellow, each cluse 2 mm, elliptic.

Distribution and habitat. *Phyla cuneifolia* is endemic to the central and western United States, where it is found in dry areas, growing in disturbed sandy soils or riverbanks and marshes. Greene (1899: 47) mentioned that it is a strongly halophilous species, common on moist subsaline or alkaline plains.

Phenology. This species is found as flowering in May, June, and July.

Taxonomic notes. *Phyla cuneifolia* is readily distinguished by its thick and coriaceous leaves, versus chartaceous or submembranous leaves in *P. betulifolia*, *P. lanceolata*, and *P. nodiflora*. The only taxon that shares similar thick and coriaceous leaves is *P. linearis*, which is differentiated by its linear

blades with connate bases, whereas *P. cuneifolia* is distinguished by its oblong to obovate blades with cuneate base.

Selected specimens examined. U.S.A. **Arizona:** Navajo, S Holbrook, 31 July 1896, *Luck s.n.* (MO). **Colorado:** Larimer, Ft. Collins, 20 June 1896, *Crandall s.n.* (MO, US). **Kansas:** Kearny, 13 mi. SW Lakin, *Rydberg 922* (MO). **Nebraska:** Phelps, N Loomis, *Tolstead 411082* (MO). **New Mexico:** Socorro, San Antonio, *Ferris 2317* (MO). **Oklahoma:** Alfalfa Co., Ingersoll, *Stevens 624* (SI). **Texas:** Tascosa, *Reverchon 3254* (MO). **Wyoming:** Platte, Uva, *Nelson 387* (US).

3. *Phyla lanceolata* (Michx.) Greene, Pittonia 4: 47. 1899. Basionym: *Lippia lanceolata* Michx., Fl. Bor.-Amer. 2: 15. 1803. *Lippia nodiflora* (L.) Michx. var. *lanceolata* (Michx.) Alph. Wood, Class-book Bot., ed. 2, 413. 1847, non Kuntze, Revis. Gen. Pl. 2: 508. 1891, nom. illeg. TYPE: U.S.A. [South] Carolina: near Ashley River, 1787–1796, *Michaux s.n.* (holotype, P not seen, P photo at SI!; isotype, P not seen, P photo at SI!). Figure 3.

Lippia nodiflora var. *acutifolia* Kuntze, Revis. Gen. Pl. 2: 508. 1891. TYPE: U.S.A. Ohio: Hamilton Co., Cincinnati, 20 Aug. 1874, *O. Kuntze 2736* (holotype, NY not seen, NY photo at SI!).

Lippia lanceolata var. *recognita* Fernald & Griscom, Rhodora 37: 178. 1935. *Phyla lanceolata* var. *recognita* (Fernald & Griscom) Soper, Trans. Roy. Canad. Inst. 34: 35. 1962. TYPE: U.S.A. Iowa: Freemont Co., 30 July 1898, *T. J. Fitzpatrick s.n.* (holotype, GH not seen, GH photo at SI!).

Phyla lanceolata f. *ahlesii* Moldenke, Phytologia 4: 56. 1952. TYPE: U.S.A. Illinois: Iriquois Co., 4 mi. S Beaverville, 5 Aug. 1950, *H. Ahles 2560* (holotype, ILL not seen, ILL photo at SI!; isotype, F not seen).

Phyla nodiflora (L.) Greene var. *texensis* Moldenke, Phytologia 27: 69. 1973, syn. nov. TYPE: U.S.A. Texas. Bexar Co., betw. 1862 & 1889, *G. Jermy s.n.* (holotype, NY not seen, NY photo at SI!).

Perennial herbs, 25–50 cm, stems erect, branches sometimes procumbent, rooting at nodes; subglabrous or slightly adpressed, strigose pubescence with malpighiaceae hairs. *Leaves* subsessile; blade elliptic, 2–7.5 × 0.5–3 cm, chartaceous, midvein prominent abaxially, secondary venation less visible; subglabrous with slightly adpressed strigose pubescence and malpighiaceae hairs, base cuneate, margins serrate to the apex, with 5 to 8 pairs of acute teeth, apex acute, sometimes slightly subobtus. *Florescences* ovoid to oblong spikes, 1 per axil, 1 × 0.7 cm at anthesis, elongating to 1.5–2.5 cm at maturity; peduncles 6–10 cm, surpassing leaves; *floral bracts* ovate, 2.5–3 mm, apex acute and contracted to acuminate or caudate, adpressed canescent pubescence with malpighiaceae hairs on abaxial surface, glabrous adaxially; *calyx* 2 mm, lobed to not more than half the length of the

calyx, membranous with thickened lateral edges, margins glabrous with scattered adpressed hairs; *corolla* pale blue, purple, or white, 4 mm, glabrous inside and outside except for a narrow band of short hairs at the base of the developed lobes. *Fruit* dry, brown to yellow, each cluse 1.2–1.5 mm, obovoid.

Distribution and habitat. *Phyla lanceolata* is widely distributed in the central and eastern United States, where it is restricted and noted from moist soil, coastal marshes, and along riverbanks in soft sands and alluvial muds, but it is also found in much drier habitats.

Phenology. This species flowers between May and September.

Taxonomic notes. *Phyla lanceolata* is distinguished by its perfectly elliptical leaves with regular margin serration, with five to eight pairs of acute teeth and its long peduncled floescences, 6–10 cm long. *Phyla nodiflora* var. *nodiflora* (L.) Greene is the most similar taxon morphologically, but its leaves are generally ovate to rhombic-ovate, spatulate or obovate. Sometimes blades are elliptic, as seen in *P. nodiflora* var. *minor* (Hook.) O'Leary & Múlgura; also, *P. nodiflora* var. *minor* has canescent pubescence with white strigose hairs (vs. subglabrous to slightly strigose leaf pubescence in *P. lanceolata*).

Moldenke (1973b) described *Phyla nodiflora* var. *texensis*, distinguishing it from the typical variety of *P. nodiflora* based on leaf morphology. However, our study of the type material indicates that this variety is the same taxon as *P. lanceolata*.

Sanders (2001: 347) observed that hybrids between this species and *Phyla nodiflora* exist in areas of sympatry between both taxa, as for example in coastal Virginia and Georgia, and in Louisiana, Oklahoma, and Texas.

Selected specimens examined. U.S.A. **Alabama:** limestone, *Isely 2824* (US). **Arkansas:** Baxter, *Hyatt 81* (MO). **California:** San Bernardino, *Roos 5306* (US). **District of Columbia:** Potomac River, *Herman 9631* (MO). **Florida:** Sarasota, *Tracy 7532* (US). **Georgia:** 1925, *Sperry 582* (US). **Illinois:** St. Clair, *Saunders 817B* (MO). **Indiana:** Bluffton, *Deam 1195* (US). **Iowa:** Fayette, *Fink 471* (US). **Kansas:** Riley, *Norton 394* (US). **Kentucky:** Robertson, *Braun 4056* (US). **Louisiana:** Iberia, *Thieret 21701* (US). **Maryland:** Dorchester, *Hotchkiss 7130* (US). **Michigan:** Wayne, 1916, *Chandler s.n.* (US). **Minnesota:** Carver Co., SSW Watertown, *G. A. Wheeler 20313* (SI). **Mississippi:** Oktibbeha, *Pollard 1310* (US). **Missouri:** St. Louis, *Taylor 5863* (MO). **Nebraska:** Saunders, Ashland, *Williams 349* (US). **New Jersey:** 1891, *Gross s.n.* (US). **New Mexico:** Chaves, *Earle 355* (US). **New York:** Cayuga, cross lake, *Muenschner 22049* (US). **North Carolina:** 1937, *Godfrey 4078* (US). **Ohio:** Greene, *Demaree 11445* (US). **Oklahoma:** Oklahoma Co., N Oklahoma City, *U. T. Waterfall 1336* (SI). **Pennsylvania:**

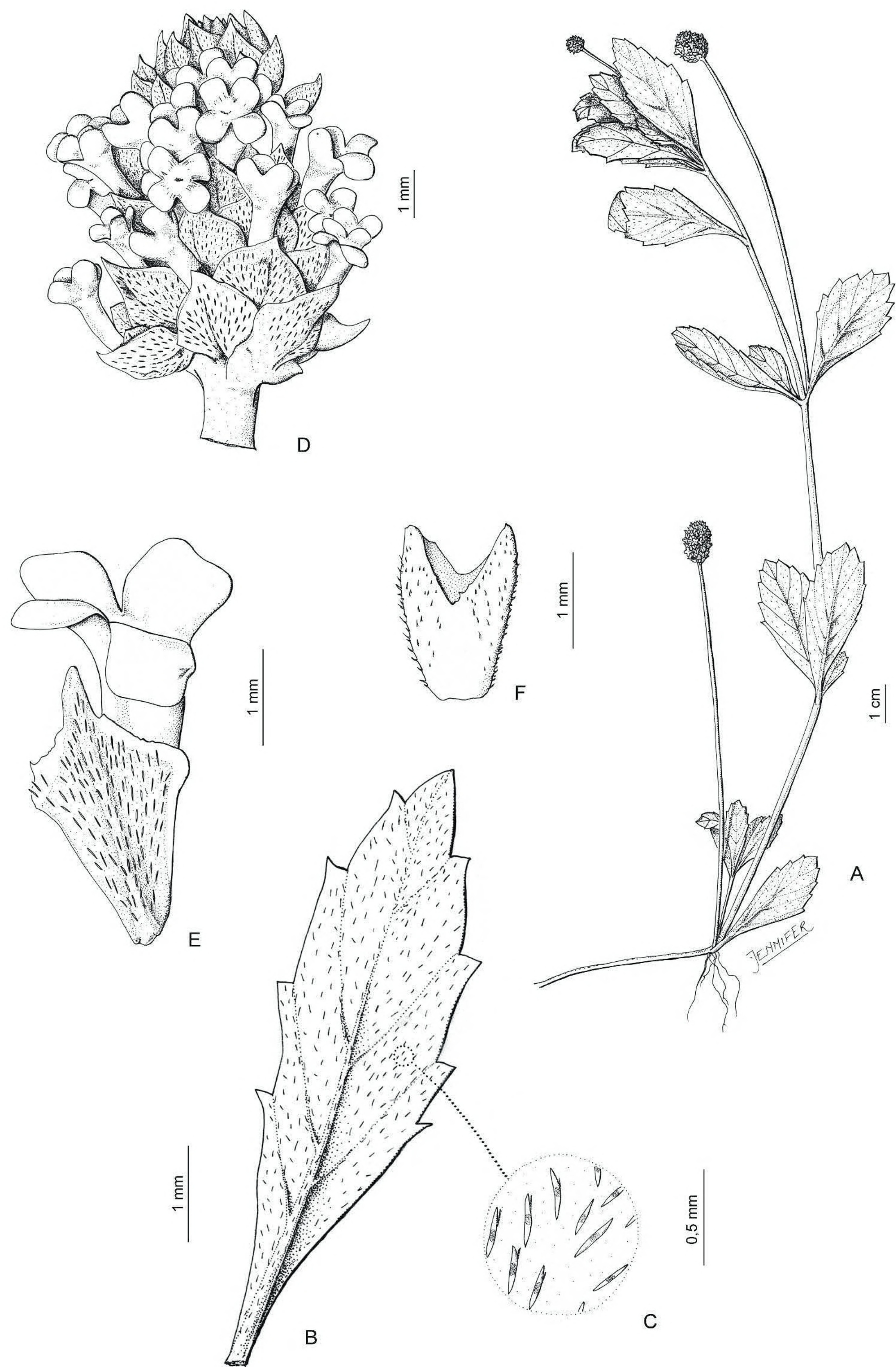


Figure 3. *Phyla lanceolata* (Michx.) Greene. —A. General aspect of plant. —B. Abaxial leaf surface. —C. Detail of pubescence of abaxial leaf surface. —D. Detail of florescence. —E. Flower with floral bract. —F. Calyx. Drawn from *Nee 43901* (SI).

Lancaster, 21 Sep. 1889, *Heller s.n.* (US). **South Carolina:** Beaufort, *Godfrey 1537* (US). **South Dakota:** 1940, *Johnson 98* (MO). **Tennessee:** Roane, *Nease 518* (US). **Texas:** Grayson Co., Sneed Environmental Research Area of Austin College, *Nee 43901* (SI). **Virginia:** Princess Anne, *Heller 1218* (US). **Washington:** 1896, *Steele s.n.* (MO). **Wisconsin:** La Crosse, *Swanson 2419* (MO).

4. *Phyla linearis* (Kunth) Tronc. & López-Pal., *Pittieria* 6: 19. 1974. Basionym: *Lippia linearis* Kunth, Nov. Gen. Sp. [H.B.K.] 2: 262, tab. 212. 1817. [1818]. TYPE: Venezuela. Sucre: Cumana, July 1800, *F. W. Humboldt & A. Bonpland* 77 (holotype, P not seen, P photo SI from F neg. 39484!; isotype, P not seen, P photo at SI!).

Perennial *herbs*, 15 cm, base woody, stems erect, branches quadrangular; glabrate with malpighiaceae hairs. *Leaves* sessile, blade linear, 1.5–3 × 0.3–0.4 cm, thick and coriaceous, midvein prominent abaxially, subglabrous with slight adpressed strigose and malpighiaceae hairs, base connate to the opposite leaf, margins entire or occasionally with 1 to 3 teeth near apex, apex acute. *Florescences* ovoid spikes, 1 per axil, 0.5 × 0.5 cm at anthesis, elongating 1.5–2 cm at maturity; peduncles 1 cm, shorter than the leaves; *floral bracts* ovate, 2 mm, acute apex, adpressed canescent pubescence on abaxial surface; *calyx* 1–2 mm, lobed to not more than half the length of the calyx, membranous with thickened lateral edges, margins glabrous with scattered adpressed hairs; *corolla* white, 2–3 mm, glabrous inside and outside except for a narrow band of short hairs at the base of the developed lobes. *Fruit* dry, brown to yellow, each cluse 1 mm, obovoid.

Distribution and habitat. *Phyla linearis* is known only from the type specimen, collected by A. Bonpland, growing in sandy soils near Cumaná, Venezuela.

Phenology. This species was collected as flowering in July.

Taxonomic notes. Examination of the type specimen of *Phyla linearis* from type photographs, as well as the description in the protologue, indicates that this taxon differs from all other taxa in *Phyla*. This species is uniquely distinguished by its linear leaf blades with the blade base connate to the opposite leaf at the stem node. It shares with *P. cuneifolia* the thick and coriaceous leaf texture, with entire margins, but occasionally with one to three teeth near the apex. It is distinguished from *P. cuneifolia* by its cuneate leaf base and oblong to obovate leaf blade.

This species was not illustrated because no material could be found; however, there is a lamina

in the *Flora de Venezuela* (López-Palacios, 1977: 487, fig. 114).

5. *Phyla nodiflora* (L.) Greene, *Pittonia* 4: 46. 1899. Basionym: *Verbena nodiflora* L., Sp. Pl. 1: 20. 1753. *Blairia nodiflora* (L.) Gaertn., Fruct. Sem. Pl. 1: 266, t. 56. 1788. *Zapania nodiflora* (L.) Lam., Tabl. Encycl. 1: 59, t. 17. 1791. *Lippia nodiflora* (L.) Michx., Fl. Bor.-Amer. (Michaux). 2: 15. 1803. *Platonia nudiflora* Raf., Med. Repos. 5: 352. 1808, nom. illeg. *Lippia nodiflora* var. *normalis* Kuntze, Revis. Gen. Pl. 2: 508. 1891. TYPE: Herb. Clifford: 11, *Verbena* 3 (lectotype, designated by Townsend [1982: 32], BM-000557561 not seen, BM-000557561 photo at SI!).

Perennial *herbs*, 3–60 cm, stems procumbent or erect, flowering branches sometimes erect, rooting at nodes; subglabrous to adpressed strigose or canescent pubescence with malpighiaceae hairs. *Leaves* subsessile; blade elliptic, obovate, spatulate, or ovate to rhombic-ovate, 0.7–8 × 0.2–3 cm, chartaceous, only midvein prominent abaxially or pinnate venation prominent abaxially; subglabrous with slightly adpressed strigose pubescence or canescent pubescence with white strigose hairs and malpighiaceae hairs; base decurrent into the petiole, or cuneate, margins entire, serrate or with teeth toward the distal part of the blade, or all along the margin; apex subobtusate or acute. *Florescences* ovoid to oblong spikes, 1 per axil, 1 × 0.5–1 cm at anthesis, elongating to 1.5–6(–7) cm at maturity; peduncles long, surpassing leaves, 3–10 cm; *floral bracts* ovate to elliptic, 2–4 mm, acute-acuminate apex, adpressed canescent pubescence on abaxial surface with malpighiaceae hairs, glabrous adaxially; *calyx* 1.5–2.5 mm, lobed to not more than half the length of the calyx, membranous with thickened lateral edges, margins with scattered adpressed and uncinatate hairs; *corolla* white, mauve, pink, pale blue, purple, or lilac, 3–4.5 mm long, glabrous inside and outside except for a narrow band of short hairs at the base of the developed lobes. *Fruit* dry, brown to yellow, each cluse 1.2–2 mm, obovoid to spherical.

Distribution and habitat. *Phyla nodiflora* is the most widely distributed taxon in *Phyla*, being found worldwide in tropical to temperate regions.

Taxonomic notes. There are three varieties of *Phyla nodiflora* principally distinguished by leaf morphology, margins, and venation. Moldenke (1939: 295) previously considered this taxon to be integrated by three varieties. These varieties are recognized here, although not under the same names.

Verdcourt (1992: 26) designated *Clayton 448* (BM) as the lectotype of *Verbena nodiflora*. The specimen had been seen by Linnaeus, so it may well be original material for the name. However, the earlier effective lectotypification was published previously by Townsend (1982).

TAXONOMIC KEY TO THE VARIETIES OF *PHYLA NODIFLORA*

- 1a. Leaf blades ovate to rhombic-ovate; pinnate venation prominent abaxially; margins serrate all along blade margin with 8 to 10 pairs of teeth or toothed toward the distal part of the blade 5c. *P. nodiflora* var. *reptans*
- 1b. Leaf blades obovate, spatulate or elliptic; only midvein prominent abaxially; margins entire or serrate toward the distal part of the blade, with 3 to 8 pairs of teeth 2
- 2a. Leaf blades elliptic or obovate, 0.5–2(–4) × 0.2–1 cm, apex mostly acute, canescent or white strigose pubescence 5b. *P. nodiflora* var. *minor*
- 2b. Leaf blades obovate, spatulate, 2–4(–7.5) × 0.5–1.5(–3) cm, apex mostly subobtusate, subglabrous or slightly adpressed strigose pubescence 5a. *P. nodiflora* var. *nodiflora*

5a. *Phyla nodiflora* (L.) Greene var. *nodiflora*.
Figure 4A–H.

Verbena capitata Forssk., Fl. Aegypt.-Arab. 10. 1775. TYPE: [Egypt.] “Rosetta ad littora Nili. Succus expreffus, multum in ufu in *Stranguria*,” s.d., *P. Forsskal* s.n. (holotype, LD not seen, LD photo at SI!).

Phyla chinensis Lour., Fl. Cochinch. 66. 1790. *Piarimula chinensis* Raf., Fl. Tellur. 2: 102. 1836 [1837]. TYPE: China. Habitat inculta prope Cantone Sinarum, s.d., *J. Loureiro 661* (holotype, P not seen, P photo at SI!).

Verbena repens Bertol., Rar. Ital. Pl. Dec. 2: 27. 1806. *Zapania repens* (Bertol.) Bertol., Rar. Ital. Pl. Dec. 3: 27. 1810. *Lippia repens* (Bertol.) Spreng., Syst. Veg. (ed. 16) [Sprengel]. 2: 752. 1825. *Lippia nodiflora* (L.) Michx. var. *repens* (Bertol.) Schauer, Prodr. (DC.) 11: 586. 1847. TYPE: [Italy.] “Sarzanæ in palustribus pratorium arenosorum di Marinella. Floret Augusto Septembri,” 1805, s. coll. (holotype, BOLO not seen, BOLO photo at SI!).

Verbena sarmentosa Willd., Enum. Hort. Berol. Alt. 632. 1809. *Lippia sarmentosa* (Willd.) Spreng., Syst. Veg. 2: 752. 1825. *Lippia nodiflora* var. *sarmentosa* (Willd.) Schauer, Prodr. 11: 585. 1847. TYPE: [India.] “Habitat in India orientali,” *Willdenow herbarium 11122* (holotype, B-W [fl.] not seen, B-W photo at SI!; isotypes, B-W [3] not seen, B-W [3] photos at SI!).

Lippia nodiflora var. *subsessilis* Bornm., Verh. Zool.-Bot. Ges. Wien 48: 615. 1898. *Phyla nodiflora* var. *subsessilis* (Bornm.) Moldenke, Phytologia 6: 447. 1959. TYPE: [Syrian Arab Republic] Palestina. Jaffa: Fruchtgarten, May 1897, *J. F. N. Bornmüller 1239b* (holotype, B not seen, B photo at SI!).

Phyla incisa Small, Fl. S.E. U.S. [Small]. 1012. 1903. *Lippia cuneifolia* (Torr.) Steud. var. *incisa* (Small) Blank., Rep. (Annual) Missouri Bot. Gard. 18: 186. 1907. *Lippia incisa* (Small) E. D. Schulz, Texas Wild Fls. 339. 1928. *Phyla nodiflora* var. *incisa* (Small) Moldenke, Phytologia 27: 69. 1973. TYPE: U.S.A.

Texas: Nueces Co., Corpus Christi, 28–31 May 1894, *A. A. Heller 1806* (holotype, NY not seen, NY photo at SI!; isotypes, MICH not seen, MICH photo at SI!, MO not seen, MO photo at SI!, NY [2] not seen, NY [2] photos at SI!, UC not seen; UC photo at SI!, US not seen, US photo at SI!).

Lippia nodiflora var. *suborbicularis* Chevall., Bull. Herb. Boissier ser. 2, 5: 443. 1905. TYPE: Algeria. Biskra, Sep. 1903, *L. Chevallier 604* (holotype, P not seen, P photo at SI!; isotypes, NY not seen, NY photo at SI!, US not seen, US photo at SI!).

Phyla nodiflora var. *longifolia* Moldenke, Phytologia 2: 22. 1941. TYPE: Honduras. Atlántida: La Ceiba, beach at Salado, 10 July 1938, *T. G. Yuncker, J. M. Koepper & K. A. Wagner 8327* (holotype, NY not seen, NY photo at SI!; isotypes, MICH not seen, MICH photo at SI!, UC not seen, UC photo at SI!, US not seen, US photo at SI!).

Phyla nodiflora f. *spathulata* Moldenke, Phytologia 4: 180. 1953. TYPE: Java. Batavia, 1902, *C. A. Backer s.n.* (holotype, BO-21889 not seen).

Phyla nodiflora var. *antillana* Moldenke, Phytologia 40: 468. 1978, syn. nov. TYPE: Virgin Islands of the United States: St. Croix, Judith’s Fancy, 17–25 Mar. 1923, *E. G. Britton, N. L. Britton & J. F. Kemp 83* (holotype, NY not seen, NY photo at SI!).

Phyla nodiflora var. *galapagensis* Moldenke, Phytologia 41: 450. 1979. TYPE: Ecuador. Galápagos Islands: Santa Cruz Island, near the Caseta, Oct. 1974, *H. H. van der Werff 1592* (holotype, NY not seen, NY photo at SI!; isotype, CAS not seen, CAS photo at SI!).

Plants 20–60 cm, stems procumbent or sometimes erect; adpressed strigose pubescence with malpighiaceus hairs. *Leaf* blade obovate, spatulate, 2–4(–7.5) × 0.5–1.5(–3) cm, only midvein prominent abaxially; subglabrous or with slightly adpressed strigose pubescence and malpighiaceus hairs; margins entire or serrate toward the distal part of the blade, with 4 to 8 pairs of acute teeth; apex subobtusate, sometimes acute. *Florescences* oblong spikes, 1 × 0.7–1 cm at anthesis, elongating to 1.5–3 cm at maturity; *corolla* white, fading to pink, 4–4.5 mm long.

Distribution and habitat. *Phyla nodiflora* var. *nodiflora* is widely distributed, found principally in the Americas, from the United States to the south, extending into Argentina and Chile. The majority of the individuals examined were from Central America (Belize, Honduras, Nicaragua, Panama, and Puerto Rico) and the Antilles (Bahamas, Barbados, Bermuda, Cayman Islands, Cuba, Dominican Republic, Guadeloupe, Haiti, and Martinique). This species is also noted from Africa (Algeria, Angola, Botswana, Egypt, Eritrea, Ethiopia, Madagascar, Malawi, Morocco, Mozambique, Senegal, Seychelles, South Africa, Swaziland, Tanzania, Togo, Tunis, Uganda, and Zaire), Asia (China, the Philippines, India, Indonesia, Iran, Japan, Saudi Arabia, and Sri Lanka), Oceania (Australia, Caroline Islands, Guam, Hawaii, New Caledonia, New Guinea, Northern Mariana, and

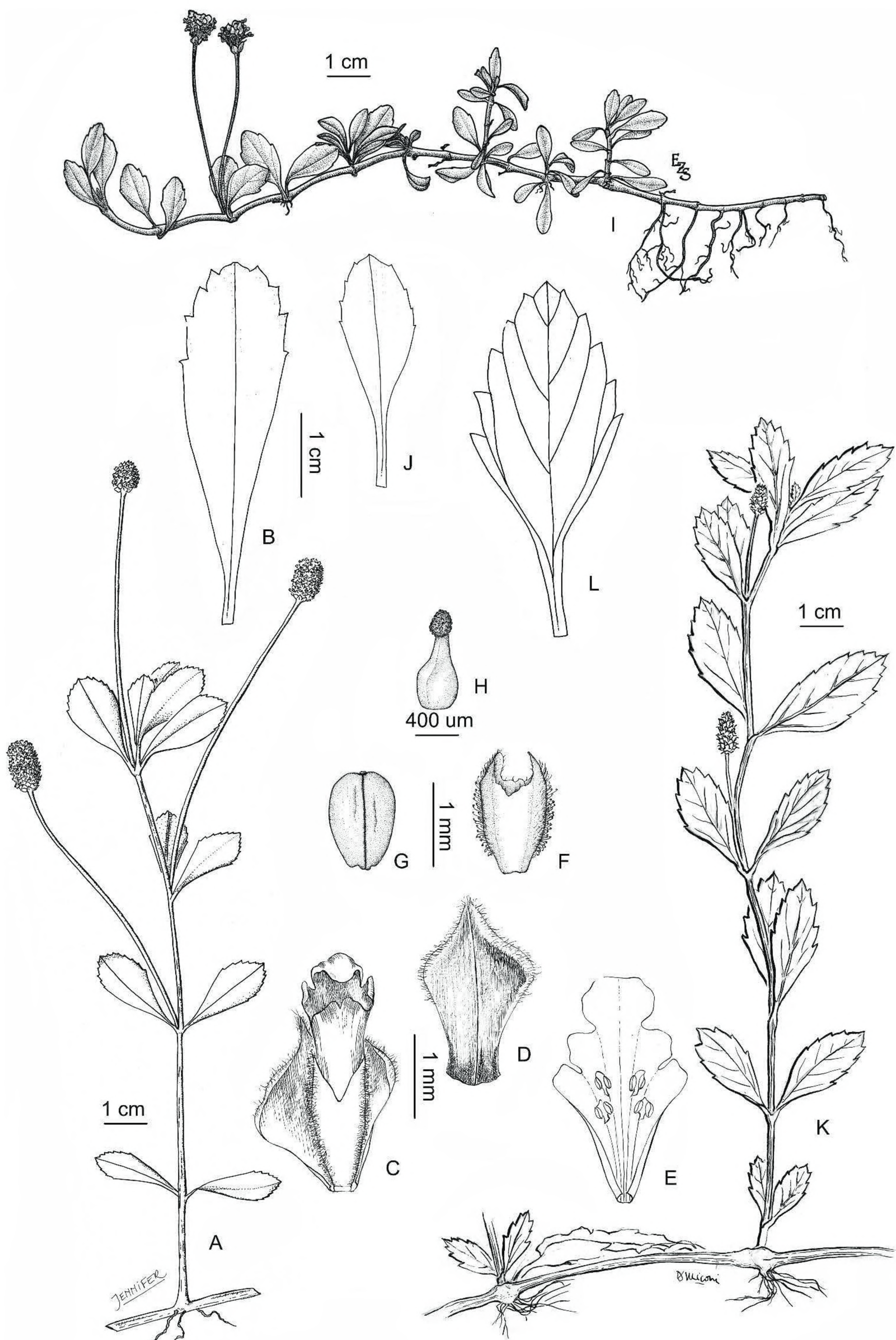


Figure 4. A–H. *Phyla nodiflora* (L.) Greene var. *nodiflora*. —A. General aspect of plant. —B. Adaxial leaf surface. —C. Flower with floral bract. —D. Floral bract. —E. Extended corolla. —F. Calyx. —G. Fruit. —H. Gynoecium. I, J. *P. nodiflora* var. *minor*. —I. General aspect of plant. —J. Adaxial leaf surface. K, L. *P. nodiflora* var. *reptans*. —K. General aspect of plant. —L. Adaxial leaf surface. Scale for J and L is the same as scale for B. A, B from *Bradley 1215* (MO); C–I, K redrawn from Troncoso and Botta (1993: 78, fig. 35); J from *Boelcke 6676* (SI); L from *Steinbach 2888* (SI).

Solomon Islands), and Europe (France and Spain). *Phyla nodiflora* var. *nodiflora* is found in disturbed soils, roadsides, and ponds, and on the borders of marshes or lakes, wherever soil has a regular water source.

Phenology. *Phyla nodiflora* var. *nodiflora* flowers in all seasons.

Taxonomic notes. There is a certain phenotype, which we do not recognize at formal taxonomical rank, but do mention as described by Small as *Phyla incisa* (Small, 1903), later treated as *P. nodiflora* var. *incisa* (Moldenke, 1973a). This corresponds to what Moldenke previously noted as *P. nodiflora* var. *longifolia*, a name synonymized herein (Moldenke, 1941). This phenotype is characterized by plants with narrow, thick-textured leaves, serrate at the apex, and has been identified in collections from Texas (Runyon 440, US) and Arkansas, U.S.A. (Demaree 17288, MO), Chihuahua, Mexico (Waterfall 12497, US), and Atlántida, Honduras (Standley 53825, US). This phenotypic variability could be related to soil condition and high temperature, because these plants were noted to grow in sandy, dry areas. We should mention one additional geographical phenotype from Sri Lanka, which has small leaves to 2 cm long and blade margins regularly crenate toward the apex (Sumithraarachchi 779A, MO; Bernardi 15673, MO).

Although the protologue of *Verbena capitata* (Forsskal, 1775: 10) did suggest that this species was not the same as *V. nodiflora* L., our study of the type specimen confirms both taxa are the same.

Moldenke (1978: 468) described *Phyla nodiflora* var. *antillana*, distinguishing it from the typical variety by the margins of its leaf blades conspicuously spreading dentate, with large, narrow, triangular teeth, sharply acute apically. However, our study of the type material indicated that this variety should not be retained because no further difference was seen between the typical variety and this phenotype.

Selected specimens examined. MEXICO. **Campeche:** Carmen, Mell 2011 (US). **Chihuahua:** Aug. 1956, Waterfall 12497 (US). **Coahuila:** Saltillo, Arsène 6334 (US). **Guerro:** Coyuca, Ancón, Hinton 5810 (US). **Jalisco:** Paso de la Troje, McVaugh 16908 (US). **México:** Zumpango, San Juan Citlaltepec, Jacquemin 1221 (SI). **Michoacán:** Río Balsas, Langlassé 145 (US). **Nuevo León:** Monterrey, Pennell 16782 (US). **Oaxaca:** Juchitán, King 352 (US). **Puebla:** Cholula, 26 Aug. 1907, Arsène s.n. (US). **Quintana Roo:** Coba, Lundell 7792 (US). **Sinaloa:** San Blas, Maliby 14 (US). **Sonora:** Fronteras, Hartman 16 (US). **Veracruz:** Laguna, Greenman 32 (US). **Yucatán:** Merida, Souza Novelo 260 (US). U.S.A. **Arkansas:** Pulaski, Demaree 17288 (MO). **California:** Sacramento, 1895, Ward s.n. (SI). **Florida:** Lee, Fort Myers, Deam 60610 (SI); Santa Rosa Co., Hwy. 87, Bradley 1215 (MO). **Georgia:** Lanier, Clewel 2595 (MO).

Louisiana: Alexandria, Ball 419 (MO). **Missouri:** 1895, Bush 471 (MO). **North Carolina:** 1885, McCarthy s.n. (US). **Oklahoma:** Payne, Stratton 213 (MO). **South Carolina:** Beaufort, Dorr 941 (MO). **Texas:** Brownsville, Runyon 440 (US). BAHAMAS. **Andros:** Coakley town, Dawson 26764 (US). **Eleuthera:** Savannah sound area, Webster 10745 (US). **Hog Island [Paradise Island]:** New Providence, Wilson 8296 (US). **Long Island:** Clarence, Hackett 156 (US). BARBADOS. **St. John:** Glenburnie, Carrington 1867 (US). BELIZE. San Pedro de Sula, Ambergris Caye, 1980, Dwyer 15056 (MO). BERMUDA. **Agar's Island:** 22 July 1913, Collins 264 (US). CAYMAN ISLANDS. George Town, Sep. 1958, Sachet 423 (US). CUBA. **Havana:** Isla de Pinos, Morton 10293 (US). **Pinar del Río:** Palme Barrens, Shafer 10623 (US). DOMINICAN REPUBLIC. **Barahona:** July 1910, Fuertes 439 (US). **Duarte:** Macoris, Boca Chica, Allard 14765 (US). **El Seibo:** Higüey, Howard 9782 (US). **Independencia:** 1980, Mejía 7137 (MO). **Puerto Plata:** Sep. 1954, Jimenez 2737 (US). **Santo Domingo:** Puerto Plata, Ekman 14516 (US). **Saona Island:** 8 July 1956, Marcano 3372 (US). GUADALOUPE. **Îlet Boissard:** Mar. 1938, Questel 663 (US). **Port-Louis:** 2 Mar. 1934, Rodriguez 2912 (SI). **Sainte-Anne:** 19 Mar. 1936, Rodriguez 4179 (SI). HAITI. Rochelois, 23 Mar. 1927, Ekman 7904 (US). **Port-de-Paix:** 21 Dec. 1928, Leonard 11023 (US). **Port-au-Prince:** Apr. 1920, Leonard 3436 (US). **Tortuga Island:** Mar. 1929, Leonard 14093 (US). HONDURAS. **Atlántida:** Tela, Standley 53825 (US). MARTINIQUE. **Sainte-Anne:** Jan. 1867/70, Hahn 1338 (SI). NICARAGUA. **Granada:** June 1869, Lévy 18 (SI). PANAMA. Canal Zone, Toro Point, 6 Oct. 1961, Duke 4328 (MO). **Los Santos:** 1962, Dwyer 2500 (MO). PUERTO RICO. Punto Cangrejos, Mar. 1914, Stevenson 1690 (US). **[Guánica:]** Guánica Lake, Mar. 1935, Sargent 11 (US). **Hamacao:** Aug. 1979, García del Llano s.n. (US). ARGENTINA. **Buenos Aires:** San Pedro, Isla Alonso, Nicora 3472 (SI). **Chaco:** Gral. Güemes, Fortín Lavalle, Pedersen 14001 (SI). **Córdoba:** Río Segundo, RN 9, Subils 986 (SI). **Corrientes:** Esquina, Krapovickas 26798 (SI). **Entre Ríos:** PN Predelta, June 2006, Sosa s.n. (SI). **Formosa:** Bermejo, La Rinconada, Arenas 3091 (SI). **Jujuy:** Santa Bárbara, Lag. San Miguel, Zuloaga 2834 (SI). **La Pampa:** Chalileo, río Salado en Santa Isabel, Troiani 3611 (SI). **Mendoza:** 10 abr. 1937, Burkart 8434 (SI). **Salta:** San Martín, Ruta 34, Zuloaga 2655 (SI). **San Juan:** 25 de Mayo, Encón, Haene 861 (SI). **San Luis:** s. loc., Pastore s.n. (SI). **Santa Fe:** Castellanos, ruta 34, Sunchales, Burkart 30602 (SI). **Santiago del Estero:** Beltrán, Maldonado 535 (SI). **Tucumán:** Leales, Chañar, Venturi 486 (SI). BOLIVIA. **Tarija:** Avilez, cerca Chocloca, Bastión 297 (SI). BRAZIL. **Rio Grande do Sul:** Torres, Burkart 25147 (SI). CHILE. **Arica and Parinacota:** Tacna, Shepard 277 (US). **Atacama:** 1985, Zöllner 12790 (MO). **Tarapacá:** Mamiña, Wiesenborn 13322 (SI). COLOMBIA. **Chocó:** Baudó, Fuchs 22123 (US). **Cundinamarca:** Usaquén, 6 abr. 1908, Apollinaire s.n. (SI). **Magdalena:** Mar. 1948, Romero 968 (US). **Nariño:** Tumaco, El Morro, Idrobo 1431 (US). ECUADOR. **Galápagos Islands:** Santa Cruz, Bentley 274 (MO). PARAGUAY. **Boquerón:** Ochoa, Mereles 5514 (MO). **Presidente Hayes:** puente Remanso, Mereles 1612 (SI). PERU. **Ancash:** 1986, Francia 145 (MO). **Arequipa:** Islay, FLSP 2453 (MO). **Cajamarca:** 1997, Lewis 17365 (MO). **Callao:** Sep. 1923, Macbride 5880 (US). **La Libertad:** Chicama valley, Graywood Smyth 66 (US). **Lambayeque:** Chiclayo, Pimentel, Fosberg 27986 (US). **Lima:** Chancay, Cerrate 1624 (MO). **Tacna:** 1986,

Dillon 4753 (MO). URUGUAY. **Rocha:** Santa Teresa, *Cabrera* 13610 (US). VENEZUELA. **Aragua:** represa Taiguaiguai, *Fernandez* 629 (SI). **Carabobo:** Urama, *Burkart* 16333 (SI). **Miranda:** Tacarigua, *Gines* 4517 (US). **Zulia:** Mocquerys, 1893, *Drake* s.n. (SI). ALGERIA. **Hamma:** s. loc., 1876, *Reboud* 1325 (MO). ANGOLA. Shella, s. loc., 1930, s. coll. (US). BOTSWANA. **North-East District:** s. loc., 1973, *Smith* 704 (MO). EGYPT. **Abu Matamir:** s. loc., 1967, *Täckholm* s.n. (MO). ERITREA. Dangollo presso Ghinda, s. loc., 1902, *Pappi* 4529 (US). ETHIOPIA. Gamo Gofa, s. loc., 1985, *Aweke* 2445 (MO). **[Harari:]** Harar, Lake Alemaya, *Bunger* 409 (US). MADAGASCAR. **Mahajanga:** s. loc., 2005, *Andriamihajarivo* 821 (MO). Toamasina, s. loc., 7 Dec. 1984, *Dorr* 3309 (US). MALAWI. **Chikwawa:** s. loc., 6 Oct. 1946, *Brass* 17998 (US). **Dowa:** s. loc., 1992, *Goyder* 3516 (MO). MOROCCO. Moulay-Bou-Selham, s. loc., 1973, *Davis* 55600 (MO). MOZAMBIQUE. **Maputo:** s. loc., 1909, *Howard* 5 (US). Lourenço Marques, s. loc., 29 Mar. 1948, *Rodin* 4156 (US). SENEGAL. **Dakar:** s. loc., *Baldwin* 5738 (US). SEYCHELLES ISLANDS. **Farquhar Atoll:** North Island, *Poore* 1365 (US). **Praslin Island:** s. loc., 1992, *Kramer* 11087 (MO). SOUTH AFRICA. Pretoria, s. loc., 1976, *Leistner* 275 (MO). SWAZILAND. Mlawula Station, 3 Nov. 1977, *Kemp* 1094 (US). TANGANYIKA [TANZANIA]. Ujiji, Mar. 1939, *Loveridge* 711 (US). TOGO. trockener, 1973, *Hiepko* 31 (MO). TUNISIA. **Gafsa:** 1908, *Pitard* 467 (US). UGANDA. **Bunyoro:** Bujenje, 1977, *Katende* 2841 (MO). ZAIRE [DEMOCRATIC REPUBLIC OF THE CONGO]. **Oriente:** Mahagi-Port, 1957, *Froment* 244 (MO). CHINA. **Guangdong:** 2002, *S. Y. Hu* 23885 (MO). PHILIPPINES. **Manila:** 1983, *Deguchi* 6344 (MO). INDIA. **Rajasthan:** Dungerpur, *Verma* 195 (MO). INDONESIA. **Tanimbar Islands:** Jamdena, *Pleyte* 1 (US). IRAN. **Khuzestan:** 1964, *Grant* 15894 (MO). JAPAN. **Kyushu:** Kagoshima, Odomari, *Ohba* 201 (SI). SAUDI ARABIA. Khoba, 1976, *Dwyer* 13638 (MO). SRI LANKA. **Batticaloa:** 1975, *Bernardi* 15673 (MO). **Northern Province:** Mantai, 1975, *Sumithraarachchi* 779A (MO). FRANCE. **Corsica:** Barcaggio, *Julien* 7 (SI). SPAIN. **Almería:** La Cañada, *Sennen* 8158 (SI). AUSTRALIA. **Cobourg Peninsula:** 1994, *Egan* 3143 (MO). CAROLINE ISLANDS. **Ulithi Atoll:** Asor islet, *Fosberg* 46388 (US). GUAM. **Apra Harbor:** 14 May 1983, *Herbst* 7152 (US). **Agana:** 13 July 1965, *Fosberg* 46295 (US). HAWAII. **Oahu:** 1980, *Degener* 35075 (MO). NEW CALEDONIA. **South Province:** Nouméa, Anse Vata, 8 Aug. 1950, *Bodenheim* 5235 (US). NEW GUINEA. **Papua:** Woodlark Island, *Brass* 28665 (US). NORTHERN MARIANA ISLANDS. **Rota:** Sinapalo, 26 Apr. 1982, *Herbst* 6768 (US). **Saipan:** Puerto Rico, *Herbst* 6879 (US). PALAU. **Peleliu:** *Emmons* 90 (US). SOLOMON ISLANDS. **Ontong Java Atoll:** Luangiua, *Bayliss-Smith* 16 (US). **Russell Islands:** Pavuvu, *Burcham* 176 (US).

5b. *Phyla nodiflora* var. *minor* (Hook.) N. O'Leary & Múlgura, comb. nov. Basionym: *Lippia nodiflora* var. *minor* Gillies & Hook., Bot. Misc. 1: 171. 1830. TYPE: Argentina. Córdoba: "ad ripas fluminis Saladillo," s.d., *J. Gillies* s.n. (holotype, K not seen, K photo at SI!). Figure 4I, J.

Lippia canescens Kunth, Nov. Gen. Sp. [H.B.K.] (quarto ed.) 2: 263. 1818. *Zappania canescens* Gilbert, Enum. Pl. Montevideo 44. 1873. *Lippia nodiflora* f. *canescens* (Kunth) Kuntze, Revis. Gen. Pl. 2: 508. 1891. *Phyla*

canescens (Kunth) Greene, Pittonia 4: 48. 1899. *Phyla nodiflora* var. *canescens* (Kunth) Moldenke, Phytologia 1: 98. 1934. TYPE: Peru. Trujillo: 1802, *F. W. Humboldt* & *A. Bonpland* s.n. (holotype, P not seen, P photo at SI!; isotype, SI!).

Lippia filiformis Schrad., Index Sem. (Gottingen): 4. 1834. *Phyla filiformis* (Schrad.) Meikle, Fl. Cyprus 2: 1249. 1985. TYPE: Chile. "from Chile, cult. Göttingen Bot. Gard.," s.d., s. coll. (holotype, GOET not seen).

Zappania nodiflora var. *rosea* D. Don in Sweet, Brit. Fl. Gard. [Sweet], 2nd. ser., 3: tab. 225. 1835. *Phyla nodiflora* var. *rosea* (D. Don) Moldenke, Phytologia 2: 22. 1941. *Lippia nodiflora* var. *rosea* (D. Don) Munz, Aliso 4(1): 97. 1958. *Lippia nodiflora* var. *rosea* (D. Don) J. F. Macbr., Publ. Field Mus. Nat. Hist., Bot. Ser. 13(5): 651. 1960, nom. illeg. TYPE: Illustration from Sweet, 1835, in Brit. Fl. Gard., 2nd. ser., 3: pt. 225 (lectotype, designated by Munir [1993: 122]).

Lippia caespitosa Rusby, Mem. Torrey Bot. Club 6: 106. 1896. *Phyla caespitosa* (Rusby) Moldenke, Revista Sudamer. Bot. 5: 2. 1937. TYPE: Bolivia. Cochabamba: below Cochabamba, 1891, *M. Bang* 1009 (holotype, NY not seen, NY photo at SI!; isotypes, MICH not seen, MICH photo at SI!, MO not seen, MO photo at SI!, NY [2] not seen, NY [2] photo at SI!, US [2] not seen, US [2] photo at SI!).

Lippia nodiflora var. *pusilla* Briq., Ark. Bot. 2(10): 19. 1904. *Phyla nodiflora* var. *pusilla* (Briq.) Moldenke, Phytologia 1: 170. 1935. TYPE: Brazil. Rio Grande do Sul: Rio Grande, 22 Nov. 1892, *C. A. Lindman* A283-1/2 (holotype, S not seen, S photo at SI!).

Lippia subterranea Rusby, Descr. S. Amer. Pl. 108. 1920. *Phyla subterranea* (Rusby) Moldenke, Revista Sudamer. Bot. 5: 2. 1937. TYPE: Peru. Mollendo, 5 Aug. 1901, *R. S. Williams* 2933 (holotype, NY not seen, NY photo at SI!).

Phyla nodiflora f. *copiapina* Acevedo, Bol. Mus. Nac. Hist. Nat. Santiago de Chile 25: 47. 1951, syn. nov. TYPE: Chile. Copiapó, frente al Río Copiapó, Nov. 1936, *M. R. Espinosa Bustos* 5 (holotype, SGO-68293 not seen, SGO-68293 photo at SI!; isotype, NY not seen, NY photo at SI!).

Plants 3–15 cm, stems procumbent, flowering branches sometimes erect; generally conspicuously canescent pubescence with white strigose and malpighiaceae hairs. *Leaf* blade elliptic or obovate, 0.5–2(–4) × 0.2–1 cm, only midvein prominent abaxially; canescent pubescence with white strigose and malpighiaceae hairs on abaxial and adaxial surfaces; margins entire or serrate toward the distal part of the blade, with 3 to 7 spreading and well-spaced shallow teeth; apex mostly acute. *Florescences* ovoid to oblong spikes, with 2 to 4 whorls of open flowers, 1 × 0.5–1 cm at anthesis, elongating to 2–3 cm at maturity; *corolla* mauve or white, fading to pink or lilac, 3–4.5 mm long.

Distribution and habitat. *Phyla nodiflora* var. *minor* is found principally in temperate South America (Argentina, Bolivia, southern Brazil, Chile, Ecuador, Paraguay, Peru, and Uruguay), in which it is presumably native (Xu et al., 2010). The existence

of specimens of this variety in other parts of the world, as for example in North and Central America (United States, Mexico, Haiti, and Dominican Republic), Australia, Europe (France and Spain, Xu et al., 2010), or Africa (Egypt; Ethiopia; Free State, South Africa), is most certainly due to unintentional introduction of this taxon and its subsequent establishment by rapid adaptative evolution (Xu et al., 2010). This variety has been noted as an invasive perennial forb widespread in Australia, threatening the productivity of the grazing industry (Price et al., 2011). *Phyla nodiflora* var. *minor* grows either on dry soils or wetter areas.

Phenology. Flowering was documented mainly between September and March, but in the northernmost distributional area, the taxon was found in flower in August.

Taxonomic notes. *Phyla nodiflora* var. *minor* is distinguished principally by its small, elliptic to obovate leaf blades, with an acute apex, as well as the white strigose pubescence on the leaves and stems, which are often densely canescent. *Phyla nodiflora* var. *nodiflora* has bigger spatulate leaves (2–4[–7.5] × 0.5–1.5[–3] cm vs. 0.5–2[–4] × 0.2–1 cm), with a mostly subobtuse apex and pubescence that is slightly adpressed strigose or glabrescent, and never canescent. Furthermore, *P. nodiflora* var. *minor* has mauve or white, fading to pink or lilac flowers, while in the typical variety the flowers are generally white.

Acevedo (1951) described *Phyla nodiflora* f. *copiapina* on the basis of its numerous leaves and florescences with whitish pubescence. Our examination of the type material of this taxon indicates that it corresponds to *P. nodiflora* var. *minor*, sharing its canescent pubescence and leaf blade size.

Selected specimens examined. MEXICO. **Hidalgo:** 1971, *Spellman* 954 (MO). HAITI. **Sud:** Etang, *Leonard* 3487 (US). U.S.A. **California:** San Joaquín, *Wolff* 2840 (MO). DOMINICAN REPUBLIC. **Monte Cristi:** Monción, *Valeur* 447 (US). ARGENTINA. **Buenos Aires:** Chapadmalal, *Hicken* 476 (SI); San Fernando, Pachecho, *Boelcke* 6676 (SI). **Catamarca:** El Alto, *Kiesling* 1273 (SI). **Chaco:** Gral. Güemes, *Fortunato* 1273 (SI). **Chubut:** Paso de los Indios, *Arroyo* 59 (SI). **Córdoba:** San Esteban, *Nicora* 1637 (SI). **Corrientes:** Mburucuyá, Ea. Sta. Teresa, *Pedersen* 1873 (US). **Entre Ríos:** Gualaguaychú, Ea. Las Casuarinas, *Romanczuk* 10 (SI). **Formosa:** Bermejo, *Fortunato* 4547 (MO). **Jujuy:** Tumbaya, *Venturi* 4903 (MO, SI, US). **La Pampa:** Hucal, Abramo, *Kaufmann* 4949 (SI). **La Rioja:** Gral Ocampo, *Biurrun* 1599 (SI). **Mendoza:** Tupungato, *Ruiz Leal* 2172 (SI). **Neuquén:** Zapala, Covunco, *Perez Moreau* 3419 (SI). **Río Negro:** San Antonio, *Correa* 10135 (SI). **Salta:** La Viña, *Novara* 8511 (SI). **San Juan:** Sarmiento, Lagunas de Guanacache, *Kiesling* 5043 (SI). **San Luis:** Paso de las Carretas, *Vignati* 7020 (SI). **Santa Fe:** Garay, Ao. El Potrero, *Fossati* 706 (SI). **Santiago del**

Estero: Fortin Tostado, June 1906, *Goubat s.n.* (SI). **Tucumán:** Tañí, Río de las Carreras, *Lillo* 7633 (US). BOLIVIA. **Cochabamba:** Colina S. Pedro, 1960, *s. coll.* 195 (US). **Santa Cruz:** Alto Mairana, *Steinbach* 6038 (SI). BRAZIL. **Rio Grande do Sul:** Gravataí, Banhados do Pacheco, *Schultz* 3492 (SI). CHILE. **Atacama:** Copiapó, *Cabrera* 11378 (SI). **Biobío:** Concepción, Hualqui, *Junge* 5927 (SI). **Coquimbo:** 1888, *Philippi* 309 (US). **Los Ríos:** Valdivia, S. José de Mariquina, *Hollermayer* 1196 (SI, US). **Maule:** Curicó, *Martcorena* 838 (SI). **Santiago:** Batuco, *Hicken* 887 (SI). **Valparaíso:** Simache, *Boelcke* 409 (SI). ECUADOR. **Guayas:** Salinas, *Svenson* 11164 (US). PARAGUAY. **Presidente Hayes:** 1994, *Zardini* 40372 (MO). PERU. **La Libertad:** Huanchaco, *Straw* 2404 (US). **Lambayeque:** Chiclayo, Pimentel, *Fosberg* 27987 (US). **Lima:** Lomas Atocongo, *Velarde* 582 (SI). URUGUAY. **Artigas:** 25 Nov. 2001, *Seijo* 2432 (SI). **Lavalleja:** 29 Nov. 2001, *Seijo* 2582 (SI). **Montevideo:** cuchilla Pereyra, *Felippone* 3297 (SI). **Rocha:** Ao. Los Indios, *Burkart* 21552 (SI). **San José:** Río Sta. Lucía, *Rosengurt B* 1399 (SI). EGYPT. **Cairo:** Kirdasa, 1975, *Helmy* 10 (MO). ETHIOPIA. Harar, Lake Alemaya, *Burger* 3440 (US). MOZAMBIQUE. **Maputo:** s. loc., 1909, *Howard* 5 (US). SOUTH AFRICA. **Albany:** 1979, *Bayliss* 8987 (MO). **Orange Free [Free State]:** Petrusburg, 25 Feb. 1981, *Herman* 283 (US). FRANCE. **Aude:** Fleury, *Julien* 4 (SI). **Hérault:** Periés, *Julien* 1 (SI). SPAIN. **Málaga:** 1906, *Gandoger s.n.* (MO). AUSTRALIA. **New South Wales:** Heatherbrae, *Prichard* 1 (SI). **Queensland:** St. Ruth's reserve, *Julien* 6 (SI). **South Australia:** St. Austin Martin's Bend, 1983, *Symon* 13087 (MO). **Victoria:** Derang Lakes, *Macdonald* 1 (SI). CAROLINE ISLANDS. **Faraulap Atoll:** *Fosberg* 47356 (US).

5c. *Phyla nodiflora* var. *reptans* (Kunth) Moldenke, *Torrey* 34(1): 9. 1934. Basionym: *Lippia reptans* Kunth, Nov. Gen. Sp. [H.B.K.] (quarto ed.) 2: 263. 1818. *Lippia nodiflora* var. *reptans* (Kunth) Kuntze, Revis. Gen. Pl. 2: 508. 1891. *Phyla reptans* (Kunth) Greene, Pittonia 4: 47. 1899. TYPE: Venezuela. Sucre: Cumana, Aug. 1800, *F. W. Humboldt & A. Bonpland* 76 (holotype, P-307282 not seen, P-307282 photo at F-39483!; isotype, B-W-11120/1 not seen, B-W-11120/1 photo at SI!). Figure 4K, L.

Verbena fruticosa Mill., Gard. Dict., ed. 8: 14. 1768. *Lippia fruticosa* (Mill.) R. W. Sanders, Harvard Pap. Bot. 5: 347. 2001. *Phyla fruticosa* (Mill.) K. Kenn. ex Wunderlin & B. F. Hansen, Bot. Explor. (Florida) 3: 38. 2003. TYPE: Mexico. Campeche: s.d., *Miller s.n.* (holotype, BM not seen, BM photo at SI!).

Lippia queretarensis Kunth, Nov. Gen. Sp. [H. B. K.] (quarto ed.) 2: 264. 1818. TYPE: Mexico. Querétaro, *F. W. Humboldt & A. Bonpland* 4196 (holotype, P not seen, P photo at SI!).

Lippia strigulosa M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 11(2): 319. 1844. *Phyla strigulosa* (M. Martens & Galeotti) Moldenke, Phytologia 2: 233. 1947. *Lippia nodiflora* (L.) Michx. var. *strigulosa* (M. Martens & Galeotti) J. F. Macbr., Publ. Field. Mus. Nat. Hist., Bot. Ser. 13(5): 651. 1960. TYPE: Mexico. Veracruz: Antigua, June 1840, *H. Galeotti* 748

(holotype, BR not seen, BR photo at SI!; isotype, P not seen, P photo at SI!).

Lippia nodiflora f. *sericea* Kuntze, Revis. Gen. Pl. 2: 508. 1891. *Phyla nodiflora* var. *sericea* (Kuntze) Moldenke, Phytologia 1: 98. 1934. *Phyla strigulosa* var. *sericea* (Kuntze) Moldenke, Phytologia 19: 435. 1970. TYPE: Trinidad and Tobago: Trinidad, 4 Apr. 1874, O. Kuntze 714 (holotype, NY not seen, NY photo at SI!).

Phyla yucatana Moldenke, Phytologia 2: 140. 1946. TYPE: Belize. Corozal, Corozal–Pachacan rd., 20 July 1933, P. H. Gentle & C. L. Lundell 4780 (holotype, NY not seen, NY photo at SI!; isotypes, CAS not seen, MICH not seen, MICH photo at SI!, NY [2] not seen, NY photo at SI!, TEX [3] not seen, TEX photo at SI!).

Phyla yucatana var. *parvifolia* Moldenke, Phytologia 2: 141. 1946. *Phyla strigulosa* var. *parvifolia* Moldenke, Phytologia 2: 233. 1947. TYPE: Mexico. Michoacán de Ocampo, Huetamo, Mal Paso, 9 May 1934, G. B. Hinton 6024 (holotype, NY not seen, NY photo at SI!; isotypes, NY not seen, NY photo SI!, US not seen, US photo at SI!).

Plants 25–60 cm, stems erect, branches diffusely branching from the base; subglabrous or slightly adpressed strigose pubescence with malpighiaceous hairs. *Leaf* blade ovate to rhombic-ovate, 3–5(–8) × 1.5–3 cm, pinnate venation prominent abaxially, secondaries ending at the sinus of teeth; slightly adpressed strigose pubescence and malpighiaceous hairs abaxially; margins serrate with 8 to 10 pairs of acute teeth all along blade margin or toothed toward the distal part of the blade; apex acute. *Florescences* ovoid to oblong spikes, 1 × 1 cm at anthesis, elongating to 4–6(–7) cm at maturity; *corolla* pale blue, purple, or white, 4 mm long.

Distribution and habitat. *Phyla nodiflora* var. *reptans* is found only in the Americas: in North America (United States and Mexico), Central America (Belize, Costa Rica, El Salvador, Guatemala, Honduras, and Puerto Rico), the Antilles (Anguilla, Barbados, Cuba, Dominican Republic, Guadeloupe, Haiti, Jamaica, Martinique, and the Virgin Islands), and in South America (Argentina, Bolivia, Brazil, Colombia, Curaçao, Ecuador, Paraguay, Peru, and Venezuela). *Phyla nodiflora* var. *reptans* was collected from wet forested areas, riverbanks, or open fields with wet soil.

Phenology. This taxon was collected in flower in all seasons except winter.

Taxonomic notes. *Phyla nodiflora* var. *reptans* is principally distinguished by its ovate to rhombic-ovate leaf blades with an acute apex, serrate margins or at least distally toothed, and a conspicuous pinnate venation abaxially. In *P. nodiflora* var. *nodiflora* and *P. nodiflora* var. *minor*, the leaf blades are elliptic to obovate, but never ovate, with a subobtusate or an acute

apex. The blade margins are entire or distally serrate, with venation abaxially indistinguishable, and generally only the midvein prominent.

Selected specimens examined. MEXICO. **Campeche:** s. loc., 1996, P. Alvaro M. 276 (MO). **Chiapas:** s. loc., 1960, Merrill King 2761 (US). **Coahuila:** Saltillo, Arsène 3423 (US). **Hidalgo:** s. loc., 1937, Fisher 3773 (US). **México:** DF, Hinton 4343 (US). **Michoacán:** Morelia, Arsène 2792 (US); Morelia, s. loc., 1909, Arsène s.n. (US). **Nuevo León:** s. loc., 1972, Dziekanowski 1752 (US). **Oaxaca:** s. loc., 1894, Nelson 336 (US). **Puebla:** s. loc., 1906, Arsène 407 (US). **Querétaro:** s. loc., 1910, Arsène 10253 (US). **San Luis Potosí:** Charcas, Lundell 5181 (US). **Sinaloa:** s. loc., 1904, Brandegee s.n. (US). **Sonora:** s. loc., 1934, Studhalte 1541 (US). **Tabasco:** Centla, Novelo 1951 (MO). **Tamaulipas:** s. loc., Merrill King 3818 (US). **Veracruz:** s. loc., 1910, Orcutt 2985 (US). **Yucatán:** s. loc., 1917, Gaumer 23670 (US). U.S.A. **Florida:** Dade, Avery 1530 (MO). **New Mexico:** Eddy, Standley 40452 (MO). **Texas:** La Joya, Walker 70 (MO). LESSER ANTILLES. **Anguilla:** s. loc., 1959, Proctor 18677 (US). BARBADOS. s. loc., 1906, Dash 137 (US). BELIZE. **Cayo:** Georgeville, Sorensen 7116 (US). **Orange Walk:** Honey camp, Lundell 553 (US). COSTA RICA. s. loc., 1965, Jimenez 3095 (US). CUBA. **Guantánamo:** s. loc., 1997, Axelrod 10439 (MO). **La Habana:** El Rosario, Juzepczuk 4078a (US). **Pinar del Río:** s. loc., 1990, Gentry 71384 (MO). **Sancti Spíritus:** s. loc., 1993, Acevedo Rodríguez 5503 (US). **Villa Clara:** Santa Clara, Smith 3124 (US). DOMINICAN REPUBLIC. **Azua:** Santo Domingo, Rose 4011 (US). **Monte Cristi:** s. loc., 1921, Abbott 1008 (US). EL SALVADOR. **San Miguel:** s. loc., 1922, Standley 20994 (US). GUATEMALA. **Alta Verapaz:** Coban, Turckheim 1259 (SI). **Izabal:** s. loc., 1922, Standley 24637 (US). **Petén:** s. loc., 1942, Steyermark 45930 (US). HAITI. **Nord-Ouest:** Baie des Moustiques, Leonard 11800 (US). HONDURAS. **Atlántida:** s. loc., 1928, Standley 55765 (US). **Comayagua:** s. loc., 1964, Standley 14266 (US). **Santa Bárbara:** s. loc., 1888, Thieme 5407 (US). **Yoro:** s. loc., 1928, Standley 55007 (US). JAMAICA. **Saint Ann:** s. loc., 1960, Adams 6718 (MO). MARTINIQUE. **Sainte-Anne:** s. loc., 1945, Stehlé 6179 (US). PUERTO RICO. Montalva, s. loc., 1915, Britton 4799 (US). Puerto Rico, Fajardo, Britton 1596 (US). U.S. VIRGIN ISLANDS. **St. Croix:** Ricksecker 223 (MO). ARGENTINA. **Buenos Aires:** Barrancas CABA, Apr. 1918, Molfino s.n. (SI). **Chaco:** Riacho Salado, Oct. 1987, Hernonen s.n. (SI). **Corrientes:** Gral. Paz, Vanni 88 (SI). **Entre Ríos:** La Paz, Burkart 30125 (SI). **Formosa:** Pirané, Guaglianone 663 (SI). **Jujuy:** Santa Bárbara, Morrone 4479 (SI). **Salta:** Orán, río Blanco, Venturi 5577 (BM, SI, US). **Santiago del Estero:** s. loc., Lillo 72 (US). **Tucumán:** Famaillá, Quebrada Leales, Venturi 2304 (SI). BOLIVIA. **Santa Cruz:** entre Guabira y Portachuelo, Zuloaga 1481 (SI); Jara, entre Nueva Motea y Portachuelo, Steinbach 2888 (SI). **Tarija:** O'Connor, Beck 9682 (SI). BRAZIL. **Mato Grosso do Sul:** Bonito, Guaicurus, Hatschbach 76114 (SI). COLOMBIA. **Atlántico:** Barranquilla, Elias 141 (US). **La Guajira:** Maicao, Roldán 1024a (MO). **Valle del Cauca:** Riofrio, Silverstone 867 (MO). CURAÇAO (NETHERLANDS). Shalome, s. loc., 1952, Arnoldo 2051 (US). ECUADOR. **Galápagos Islands:** Kreck Bay, Stewart 3302 (SI). **Guayas:** Guayaquil, Stork 8977 (US). **Manabí:** San Jacinto, Roig 9853 (SI). PARAGUAY. **Alto Paraguay:** Cerro León, Laguna Nueva Misión, Schinini 18015 (G). **Boquerón:** Tinfunké, Mereles 521 (SI). **Central:** lago Ypacarai, Hassler 11567 (BM, US).

Concepción: s. loc., 1901–1902, *Hassler* 7438 (BM, G). **Ñeembucú:** Cerrito, *Hassler* 1338 (BM, G). **Presidente Hayes:** Ea. Zalazar, *Zardini* 45976 (SI). PERU. **La Libertad:** s. loc., 1934, *Graywood Smyth* 28 (US). **Lambayeque:** de Chiclayo a Reque, *Scolnik* 1244 (SI). **Lima:** s. loc., 1976, *Gentry* 16457 (MO). **Piura:** s. loc., 1955, *Böcher* 278 (US). **San Martín:** s. loc., 1937, *Belshaw* 3168 (US). **Tumbes:** s. loc., 1968, *Simpson* 583 (US). VENEZUELA. **Anzoátegui:** Bruzual, *Delascio* 12902 (MO). **Carabobo:** Pto. Cabello & El Patito, *Pittier* 8782 (SI). **Falcón:** Paraguaná, Pueblo Nuevo, *Tamayo* 1091 (US). **Lara:** El Tocuyo, *Tamayo* 3353 (SI). **Mérida:** Playa de Cabo Blanco, *Pittier* 10187 (US). **Nueva Esparta:** Isla de Margarita, *Steyermark* 130972 (MO).

INCERTAE TAXA

Walpers (1845: 49) mentioned four varieties of *Phyla nodiflora* (sub nom. *Lippia nodiflora*), as *L. nodiflora* var. *arenaria* Walp., *L. nodiflora* var. *debilis* Walp., *L. nodiflora* var. *vulgaris* Walp., and *L. nodiflora* var. *umbrosa* Walp. No specimen information was cited and the location of Walpers's types is unknown (Stafleu & Cowan, 1988). A similar situation occurred with another taxon by Walpers whose type material was not found (*L. uncinuligera* Nees ex Walp., Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 19, Suppl. 1: 377. 1843. TYPE: Chile, Melipilla, s.d, s. coll.). The fact that this last specimen is from Chile makes it probable that it might be a synonym of *P. nodiflora*, but the absence of type material makes it impossible to ascertain.

Lippia nodiflora f. *brevipes* Kuntze, Revis. Gen. Pl. 2: 508. 1891. TYPE: Java: Samarang, Bombay.

The type material of this taxon has not been located and is not housed in NY. It may be related to *Phyla nodiflora* var. *nodiflora* since this taxon is the only one known to be distributed in Java.

Lippia litoralis Phil., Anales Univ. Chile 90: 624. 1895. TYPE: Chile. Constitución, "in litore arenoso ad Constitucion," 1885–86, *P. Ortega* s.n.

The type material of this taxon was not found in the herbaria at SGO or P. In his protologue, Philippi mentions its similarity to *Lippia canescens* Kunth [= *Phyla nodiflora* var. *minor* (Hook.) N. O'Leary & Múlgura].

Lippia nodiflora f. *pseudo-sarmentosa* A. Reyn., Bull. Soc. Bot. Fr. 62: 205. 1915.

No type material was found for this taxon, with collections investigated at FI, G, and NICE.

EXCLUDED TAXA

The following two taxa, *Lippia dulcis* Trevir. and *L. stochaedifolia* (L.) Kunth, were treated by three previous authors under *Phyla* (López Palacios,

1977; Pool, 2001; Méndez Santos, 2003). However, these are considered here to be better placed under *Lippia*, given that both species lack malpighiaceae hairs, which are characteristic of the genus *Phyla*, and are woody shrubs rather than the herbaceous habit noted for all *Phyla* species considered herein. Phylogenetic studies (Marx et al., 2010) show that both taxa lie within a *Lippia* clade and are not nested within the five *Phyla* taxa sampled.

Lippia dulcis Trevir., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 13(1): 187. 1824. *Phyla dulcis* (Trevir.) Moldenke, Torreya 34: 9. 1934. TYPE: Cuba. Cultivated from seed sent by Antonius de la Ossa, grown in the garden of George Staunton, s.d., s.n. (holotype, BHU not seen; isotype, NY not seen, NY photo at SI!).

Verbena stoechadifolia L., Sp. Pl. 1: 19. 1753. *Zappania stoechadifolia* (L.) Juss., Pers. Syn. Pl. 2: 140. 1806. *Lippia stoechadifolia* (L.) Kunth, Nov. Gen. Sp. [H.B.K.] (quarto ed.) 2: 265. 1817 [1818]. *Panope stoechadifolia* (L.) Raf., Fl. Tellur. 2: 103. 1836. *Phyla stoechadifolia* (L.) Small, Bull. Torrey Bot. Club 36: 162. 1909. TYPE: Herb. A. van Royen 913. 13–121 (neotype, designated by Méndez & Cafferty [2001: 1140], L not seen, L photo at SI!).

Literature Cited

- Acevedo R. de Vargas. 1951. Índice específico de las Verbenaceae chilenas, nuevas o críticas del herbario del Museo Nacional. Bol. Mus. Nac. Hist. Nat. Chile 25: 35–72.
- Atkins, S. 2004. Verbenaceae. Pp. 449–468 in K. Kubitzki (editor), The Families and Genera of Vascular Plants. VII. Springer Verlag, Berlin.
- Bentham, G. 1839. Enumeration of plants collected by Mr. Schomburgk in British Guiana. Ann. Nat. Hist. ser. 1. 2: 445–451.
- Bir, S. S. & M. Sidhu. 1980. Cyto-palynological studies on weed flora of cultivable lands of Patiala District (Punjab). J. Palynol. 16: 85–105.
- Brako, L. & J. L. Zarucchi. 1993. Verbenaceae, *Lippia*. Pp. 1173–1175 in Catalogue of the Flowering Plants and Gymnosperms of Peru. Monogr. Syst. Bot. Missouri Bot. Gard. 45.
- Briquet, J. 1895. Verbenaceae. Pp. 132–182 in A. Engler & K. Prantl (editors), Nat. Pflanzenfam. IV(3a). Dunker und Humboldt, Berlin.
- Covas, G. & B. Schnack. 1946. Número de cromosomas en Antófitas de la region de Cuyo (República Argentina). Rev. Argentina Agron. 13: 153–166.
- Forsskal, P. 1775. *Verbena*. Pp. 167–236 in Flora Aegyptiaco-Arabica 10. Möller, Copenhagen.
- Gibson, D. N. 1970. Verbenaceae. Pp. 167–236 in P. C. Standley & L. O. Williams (editors), Flora of Guatemala. Fieldiana, Bot. Ser. 24(9).
- Greene, E. L. 1899. Neglected generic types I. Pittonia 4: 45–49.
- Hickey, L. J. 1974. Clasificación de la arquitectura de las hojas de dicotiledóneas. Bol. Soc. Argent. Bot. 16: 1–24.
- Jansen-Jacobs, J. 1988. Verbenaceae, *Lippia*. Pp. 48–55 in A. R. Görts-Van Rijn (editor), Flora of the Guianas.

- Series A: Phanerogams, fasc. 4, 148. Koeltz Scientific Books, Königstein.
- Jørgensen, P. M. & S. León-Yáñez. 1999. Verbenaceae. Pp. 936–943 in *Catálogo de las Plantas Vasculares del Ecuador*. Monogr. Syst. Bot. Missouri Bot. Gard. 75.
- Lawrence, G. H. 1951. *Taxonomy of Vascular Plants*. Macmillan, New York.
- Lewis, W. H. 1961. Chromosome numbers for five American species of *Callicarpa*, *Lantana*, and *Phyla* (Verbenaceae). Southw. Naturalist 6: 47–48.
- López-Palacios, S. 1977. Verbenaceae, *Phyla*. Pp. 481–503 in *Flora de Venezuela*. Talleres Gráficos Universitarios, Mérida.
- Loureiro, J. 1790. Tetrandria Monogynia. Pp. 63–90 in *Fl. Cochinch.* Typis et expensis academicis, Lisbon.
- Macbride, J. F. 1960. Verbenaceae. Pp. 609–721 in *Flora of Perú*. Publ. Field Mus. Nat. Hist. Bot. Ser. 13 (5/2).
- Marx, H., N. O'Leary, Y. Yuan, P. Lu-Irving, D. Tank, M. E. Múlgura & R. Olmstead. 2010. A molecular phylogeny and classification of Verbenaceae. *Amer. J. Bot.* 97(10): 1647–1663.
- Méndez Santos, I. E. 2003. Verbenaceae. Pp. 1–126 in W. Greuter & R. Rankin Rodríguez (editors), *Flora de la República de Cuba* 7. Koeltz Scientific Books, Königstein.
- Méndez Santos, I. E. & S. Cafferty. 2001. Typification of Linnean names of taxa of Verbenaceae s. str. described from the Greater Antilles. *Taxon* 50: 1137–1141.
- Moldenke, H. N. 1939. The Verbenaceae and Avicenniaceae of Trinidad and Tobago. *Lilloa* IV: 284–336.
- Moldenke, H. N. 1941. Novelties in the Eriocaulaceae and Verbenaceae. *Phytologia* 2: 6–32.
- Moldenke, H. N. 1942. Verbenaceae *Phyla*. Pp. 55–62 in C. L. Lundell & collaborators. *Fl. Texas* [C.L. Lundell et al.] 3. University Press, Southern Methodist Press, and Texas Research Foundation, Renner, Texas.
- Moldenke, H. N. 1973a. Part IX: Family 168. Verbenaceae. Pp. 59–66 in R. E. Woodson, R. W. Schery & collaborators. *Flora of Panama*. Ann. Missouri Bot. Gard. 60(1).
- Moldenke, H. N. 1973b. Notes on new and noteworthy plants LXIII. *Phytologia* 27: 63–73.
- Moldenke, H. N. 1978. Notes on new and noteworthy plants CXVII. *Phytologia* 40: 468.
- Moldenke, H. N. 1983. Verbenaceae. Pp. 196–487 in M. D. Dassanayake & F. A. Fosberg (editors), *Revis. Handb. Fl. Ceylon* 4. Amerind Publishing Co. Pty. Ltd., New Dehli.
- Múlgura, M. E. 2003. Verbenaceae, parte 1, subfamilia Verbenoideae, tribu Lantaneae, parte A. *Fl. Fanerog. Argentina*, fasc. 84, 253: 40–43.
- Múlgura, M. E., S. Martínez, S. Atkins & A. Rotman. 2002. Morfología de las inflorescencias en Verbenaceae, Verbenoideae III: Tribu Lantaneae p.p. *Darwiniana* 40: 1–15.
- Munir, A. A. 1993. A taxonomic revision of the genus *Phyla* Lour. (Verbenaceae) in Australia. *J. Adelaide Bot. Gard.* 15(2): 109–128.
- Pool, A. 2001. Verbenaceae. *Phyla*. Pp. 2517–2519 in *Flora de Nicaragua*. Monogr. Syst. Bot. Missouri Bot. Gard. 85(3).
- Price, J., M. Macdonald, C. Gross, R. Whalley & I. Simpson. 2011. Vegetative reproduction facilitates early expansion of *Phyla canescens* in a semi-arid floodplain. *Biol. Invasions* 13: 285–289.
- Rzedowsky, J. & G. Calderón de Rzedowsky. 2002. *Flora del Bajío y de Regiones Adyacentes*. Fasc. 100. Instituto de Ecología, Pátzcuaro, Mexico.
- Sanders, R. W. 2001. The genera of Verbenaceae in the southeastern United States. *Harvard Pap. Bot.* 5(2): 303–358.
- Schauer, J. C. 1847. Verbenaceae. Pp. 522–700 in A. L. de Candolle (editor), *Prodr.* 11. Sumptibus sociorum Truttel et Würtz, Paris.
- Sharma, A. K. 1970. Annual report. 1967–1968. *Res. Bull. Cytogen. Lab. Dept. Bot. Univ. Calcutta* 2: 1–50.
- Small, J. K. 1903. *Phyla*. P. 1012 in *Flora of the Southeastern United States*, ed. 1. New York.
- Stafleu, F. A. & R. S. Cowan. 1988. *Taxonomic Literature*, Vol. 7, ed. 2. Bohn, Scheltema & Holkema, Utrecht.
- Suttill, T. A. & G. A. Allen. 1992. Morphological and chromosomal variation in *Dodecatheon pulchellum* (Primulaceae). *Canad. J. Bot.* 70: 2476–2483.
- Townsend, C. C. 1982. Verbenaceae. Pp. 31–35 in P. H. Davis (editor), *Fl. Turkey* 7.
- Troncoso, N. S. 1965. Verbenaceae, *Phyla*. Pp. 125–127 in A. L. Cabrera (editor), *Flora de la Provincia de Buenos Aires V*. Colecc. Ci. Inst. Nac. Tecnol. Agropecu. 4(3).
- Troncoso, N. S. 1979. Verbenaceae, *Phyla*. Pp. 285–288 in A. Burkart (editor), *Flora Entre Rios*. Colecc. Ci. Inst. Nac. Tecnol. Agropecu. 6(5).
- Troncoso, N. S. & S. M. Botta. 1993. Verbenaceae, *Phyla*. Pp. 76–79 in A. L. Cabrera (editor), *Flora de la Provincia de Jujuy*. Colecc. Ci. Inst. Nac. Tecnol. Agropecu. 13(9).
- Verdcourt, B. 1992. Verbenaceae. Pp. 1–155 in R. M. Polhill (editor), *Flora of Tropical East Africa*. A. A. Balkema, Rotterdam.
- Walpers, G. G. 1845. Verbenaceae. Pp. 5–134 in *Repert. Bot. Syst.* 4. Sumtibus Friderici Hofmeister, Leipzig.
- Wiggins, I. L. 1980. Verbenaceae, *Phyla*. Pp. 530–531 in *Flora of Baja California*. Stanford University Press, Palo Alto.
- Wiggins, I. L. & D. M. Porter. 1971. Verbenaceae, *Phyla*. Pp. 494–496 in *Flora of the Galápagos Islands*. Stanford University Press, Palo Alto.
- Xu C. Y., J. Mic, M. Fatemi, C. Girod, R. Klinken, C. Gross & S. Novak. 2010. Phenotypic divergence during the invasion of *Phyla canescens* in Australia and France: Evidence for selection-driven evolution. *Ecol. Lett.* 13(1): 32–44.

APPENDIX 1. List of species and index to collectors. Collections are listed alphabetically by the collector's last name. The number in parentheses, after the collector's number, corresponds to the species number in the species list. Specimens are located in BM, G, MO, NY, SI, and US.

1. *Phyla betulifolia* (Kunth) Greene
2. *Phyla cuneifolia* (Torr.) Greene
3. *Phyla lanceolata* (Michx.) Greene
4. *Phyla linearis* (Kunth) Tronc. & López-Pal.
- 5a. *Phyla nodiflora* (L.) Greene var. *nodiflora*
- 5b. *Phyla nodiflora* (L.) Greene var. *minor* (Hook.) N. O'Leary & Múlgura
- 5c. *Phyla nodiflora* (L.) Greene var. *reptans* (Kunth) Moldenke

Abbott 1008 (5c), 1766 (5a), 2869 (5a); **Abrams** 2527 (3); **Acevedo Rodriguez** 5503 (5c); **Adams** 6718 (5c); **Ahumada**

4625 (5c), 8489 (5c), 8804 (5c), 8977 (5b); **Albert** 2090 (2); **Allard** 14765 (5a), 14780 (5a); **Allison** 132 (3), 278 (5a); **Alston** 6360 (5c); **Alvarez** 507 (5b); **Andriamihajarivo** 821 (5a); **Antuña** 72 (5c); **Apollinaire** s.n. (5a); **Arbo** 247 (5b), 8941 (5c); **Archer** 1402 (1); **Arenas** 2256 (5c), 3091 (5a); **Armer** 5532 (5c); **Arndt** 19 (5a); **Arnoldo** 2051 (5c); **Arroyo** 59 (5b); **Arsène** s.n. (5a), s.n. (5c), 92 (5c), 407 (5c), 936 (5a), 2792 (5c), 3423 (5c), 6334 (5a), 8532 (5c), 10253 (5c), 10366 (5c); **Asplund** 111 (5a), 5641 (5b), 11105 (5a), 13890 (5c), 14293 (1); **Avery** 1530 (5c); **Aweke** 2442 (5a), 2445 (5a); **Axelrod** 10439 (5c).

Babcock s.n. (3); **Bacigalupo** 11658 (5b); **Bailey** 1616 (1); **Baker** 287 (5c), 1439 (5a); **Bakery Van Herman** 1964 (5a); **Bakery Wilson** 2230 (5a); **Baldwin** 5738 (5a); **Ball** 419 (5a); **Baltars** 2768 (3); **Barclay** 402 (5c); **Barrell** 162–73 (3); **Barren** s.n. (3); **Bartlett** 16371 (1), 19691 (5b); **Bartsch** s.n. (3); **Basti6n** 297 (5a); **Bayliss** 8987 (5b); **Bayliss-Smith** 16 (5a); **Bazzi** 345 (5c); **Bechdolt** s.n. (3); **Beck** 6462 (5c), 9682 (5c), 11517 (5c), 11594 (5c), 19525 (1), 20455 (1); **Belshaw** 3168 (5c); **Bentley** 274 (5a); **Berlandier** 316 (5a); **Bernard** 497 (5b); **Bernardi** 15673 (5a); **Biurrum** 1599 (5b); **B6cher** 278 (5c); **Bodenheim** 5235 (5a); **Boelcke** 409 (5b), 1532 (5b), 5046 (5b), 6676 (5b); **Bogusch** 11915 (5c); **Boom** 7194 (1); **Bourgeau** 548 (5a); **Bowes** 29 (5b); **Brace** 5208 (5a); **Bradley** 1215 (5a); **Brandeggee** s.n. (5c); **Brass** 17998 (5a), 28665 (5a); **Braun** s.n. (3), 1716 (3), 2519 (3), 3170 (3), 4056 (3); **Braunton** 447 (3), 499 (3), 627 (3); **Breteler** 4359 (5c); **Brinker** 370 (5a); **Britton** 1055 (1), 1596 (5c), 4799 (5c), 14520 (5a), 15400 (5a); **Brizuela** 1463 (5b); **Broadway** s.n. (1), 7206 (1), 8954 (1); **Brooks** 7 (5a), 17773 (5a); **Bruner** s.n. (3); **Buchanan** 339 (5a); **Buchtien** s.n. (5b), 12354 (5a); **Bunger** 409 (5a); **Burcham** 176 (5a); **Burger** 3440 (5b); **Burkart** 468 (5b), 3964 (5b), 4489 (5b), 6791 (5c), 8356 (5b), 8434 (5a), 9345 (5b), 13198 (5a), 16333 (5a), 20220 (5a), 21552 (5b), 21555 (5a), 23096 (5b), 23794 (5b), 24906 (5b), 25147 (5a), 27049 (5c), 27053 (5c), 27054 (5c), 27361 (5b), 28073 (5b), 28976 (5b), 30100 (5b), 30124 (5c), 30125 (5c), 30127 (5c), 30602 (5a); **Bush** 471 (5a), 1412 (5a), 4070 (3).

Cabral 741 (5a); **Cabrera** 2130 (5b), 4247 (5b), 9860 (5b), 11378 (5b), 13610 (5a), 20075 (5a), 20269 (5c), 23549 (5b), 24028 (5c), 27550 (5c), 27562 (5b), 29674 (5b), 29861 (5c), 32242 (5c), 33626 (5c), 34568 (5b), 34617 (5b); **Calder6n** 2380 (5c); **Camp** E-3549 (5c); **Canby** 841 (3), 2665 (3); **Cantino** 391 (5c); **Carrington** 1867 (5a); **Cer6n** 6711 (5c); **Cerrate** 1624 (5a); **Chalukian** 1995 (5b); **Chandler** s.n. (3), 7012 (5c), 7012a (5c); **Chase** 7724 (5a); **Clarke** 3861 (1); **Clemente** 4451 (5c); **Clewel** 2595 (5a); **Collins** 264 (5a); **Colonnello** 1806 (1); **Congdon** s.n. (3); **Copeland** 3501 (5b); **Correa** 6 (5b), 7701 (5c), 10130 (5b), 10135 (5b), 10521 (5b); **Correll** 14945 (5c), 48746 (5a); **Corwen** s.n. (2), 402 (2); **Cory** 53264 (3); **Crandall** s.n. (2); **Crawford** s.n. (3); **Crespo** 1808 (5b); **Croat** 2455 (5a), 19147 (1), 23646 (5c); **Cuezzo** 1743 (5a); **Cunquero** 331 (5b); **Curtiss** 706 (5a).

Daniels 406 (2); **Darbyshire** 805 (5a); **D’Arcy** 2014 (5a), 15292 (5a); **Dash** 137 (5c); **Davidson** 232 (3); **Davis** 55600 (5a); **Dawson** 1640 (5a), 26764 (5a), 26770 (5a), 26855 (5a); **Deam** 1195 (3), 60610 (5a); **Decary** 12873 (5a); **Degen** 2962 (5a); **Degener** 35075 (5a); **Deguchi** 6344 (5a); **Delascio** 12902 (5c); **Demaree** 6943 (3), 8355 (3), 11445 (3), 14087 (3), 17288 (5a); **Dillon** 4753 (5a); **Dodge** 99 (5c); **Dodson** 12978 (5c); **Donnell Smith** s.n. (3); **Dorr** 941 (5a), 3309 (5a); **Dowell** 4172 (1); **Drake** 114 (5a), 918 (5a); **Drake** s.n. (5a), s.n. (5c); **Drummond** 254 (3); **Duarte** 7317 (1); **Duke** 4328 (5a), 9663 (5a); **Duss** 2941 (5a), 415 (5a); **Dwyer** 2500 (5a), 13638 (5a), 15056 (5a); **Dzieskanowski** 1752 (5c).

Earle 355 (3); **Eastwood** 124 (2); **Edwin** 3783 (5a); **Egan** 3143 (5a); **Eggers** 1537 (5a), 7077 (5c), 14275 (1); **Eggert**

s.n. (3); **Ek** 133 (3); **Ekman** 28 (5c), 5645 (1), 7531 (5a), 7904 (5a), 13750 (1), 14516 (5a), 16360 (5c), 16499 (5c); **Elias** 141 (5c); **Emmons** 90 (5a); **Engelmann** s.n. (2); **Espina** 2501 (5a); **Evans** 243 (5a), 1672 (5a); **Evans Schultes** 46-140 (1), 6597 (1), 8512 (1); **Eyerdam** 561 (5a), 23711 (5b); **Ezcurra** 5 (5b).

Fabris 3120 (5c); **Fairchild** 108 (5b); **Faircloth** 640 (5a); **Falanruw** 1285 (5a); **Felippone** 2615 (5b), 3297 (5b), 5647 (5b); **Fernald** 11126 (3), 12783 (3); **Fernandez** 629 (5a); **Fernandez Casas** 4286 (5c); **Ferraro** 986 (5b); **Ferris** 2317 (2), 3091 (5c); **Fiebrig** 2518 (5a); **Fink** 471 (3); **Fischer** 105 (5b), 140 (5c), 3339 (5c), 3773 (5c); **FLSP** 2453 (5a); **Flyr** 1496 (2); **Fortunato** 1273 (5b), 2289 (5c), 2502 (5a), 4547 (5b); **Fosberg** 27986 (5a), 27987 (5b), 28201 (5a), 28950 (1), 31237 (5a), 46295 (5a), 46296 (5a), 46388 (5a), 47356 (5b), 47615 (5a), 59174 (5c); **Fossati** 706 (5b), 950 (5a); **Fraga** 8 (5b); **Francia** 145 (5a); **Fredholm** 6075 (5a); **Froment** 244 (5a); **Frye** 2347 (5c); **Fuchs** 22123 (5a); **Fuertes** 439 (5a), 1133 (5a).

Galeotti 795 (5a); **Gandoger** s.n. (5b); **Gapson** s.n. (3); **Garcia** 88 (5a); **García del Llano** s.n. (5a); **Gardner** 1049 (1); **Gaumer** 621 (5a), 1876 (5a), 23670 (5c); **Gentry** 171 (5c), 8522 (5c), 8568 (5a), 16457 (5c), 54827 (5c), 71384 (5c); **Giardelli** 629 (5b); **Gines** 4517 (5a), 4577 (5a); **Godfrey** 327 (5a), 719 (3), 1537 (3), 4078 (3); **Goldsmith** 110 (5a); **Goll** 547 (5c), 773 (5c); **Gooding** 578 (2); **Goodman** 3052 (2); **Goubat** s.n. (5b); **Goyder** 3516 (5a); **Graham** 363 (1); **Grant** 15894 (5a); **Graywood Smyth** 28 (5c), 66 (5a); **Greenman** 32 (5a); **Griffiths** 6477 (5c); **Grisol** s.n. (1); **Gross** s.n. (3); **Grück** s.n. (5a); **Guaglianone** 586 (5a), 663 (5c), 1300 (5b), 2194 (5c); **Gunckel** 17313 (5b).

Haas 179 (3); **Hackett** 156 (5a); **Haene** 30 (5b), 861 (5a); **Hagelund** 5754 (5a); **Hahn** 1338 (5a), 4841 (1); **HAL** 5089 (5b), 9834 (5b); **Hanson** 508 (5c); **Harley** 25868 (1); **Hartley** 5040 (3); **Hartman** 16 (5a); **Hassler** 1338 (5c), 7438 (5c), 7553 (1), 11567 (5c); **Hatschbach** 30468 (5c), 76114 (5c); **Haught** 2825 (1); **Hayden** 9425 (3); **Heller** s.n. (3), 1218 (3), 1920 (5c), 6267 (5a); **Helmy** 10 (5b); **Henderson** 68-492 (3), 94-769 (3); **Henty** 49731 (5a); **Herbst** 6768 (5a), 6879 (5a), 7152 (5a); **Herman** 283 (5b), 9631 (3); **Hernandez Magaña** 6049 (5c); **Hernonen** s.n. (5c); **Herter** 18 (5b), 8953 (5b); **Hetz** s.n. (2); **Hicken** s.n. (5b), 9 (5b), 65 (5b), 108 (5b), 109 (5b), 111 (5c), 338 (5b), 476 (5b), 479 (5b), 495 (5b), 887 (5b), 888 (5b); **Hiepkö** 31 (5a); **Hill** 15635 (3), 22451 (5c), 27103 (1); **Hinton** 4343 (5c), 5695 (5c), 5810 (5a), 13823 (5a), 14523 (5a); **Hoffman** 1011 (1); **Holdridge** 885 (5a), 2101 (5a); **Hollermayer** 1196 (5b); **Horowitz** 3398 (5c); **Horr** E230 (3), 3484 (3), 4300 (3); **Hotchkiss** 7130 (3); **Houghton** 3726 (5a); **Howard** 5 (5c), 8588 (5a), 9594 (5c), 9771 (5a), 9782 (5a); **Hu** 23885 (5a); **Hudson** 909 (5a), 943 (5c); **Hunziker** 1314 (5b), 12849 (5c); **Hurrell** 4908 (5b); **Hyatt** 81 (3); **Hylan** 31 (3).

Idrobo 1431 (5a); **Irigoyen** 157 (5b); **Irwin** 772 (1); **Isely** 2824 (3).

Jack 6136 (5c); **Jacquemin** 1221 (5a); **Jahn** 1224 (5a); **Jennings** 146 (5a); **Jetterman** s.n. (2); **Jimenez** 199 (5c), 839 (5a), 1136 (5a), 1305 (5a), 2737 (5a), 3095 (5c); **Johnson** 89B (2), 98 (3); **Jorgensen** 2472 (5a); **Juárez** 1534 (5a); **Julien** 1 (5b), 2 (5b), 3(5b), 4 (5b), 5 (5b), 6 (5b), 7 (5a), 8 (5a), 9 (5b), 10 (5b), 11 (5b); **Junge** 5927 (5b); **Juzepeczuk** 4078a (5c), 4078b (5a).

Katende 2841 (5a); **Kaufmann** 4949 (5b); **Keally** s.n. (5c); **Kearney** 2033 (3); **Kemp** 1094 (5a); **Kiesling** 1273 (5b), 4926 (5b), 5043 (5b), 5382 (5b); **Killip** 20 (5c), 6234 (5c), 13614 (5a), 41673 (5a), 42572 (5a); **King** 352 (5a), 1699 (5a); **Knowlton** 99 (2); **Kral** 27498 (5a); **Kramer** 11087 (5a);

Krapovickas 687 (5b), 1225 (5a), 11785 (5b), 22268 (5b), 26798 (5a), 27088 (5b), 30865 (5c).

Lanfranchi 87 (5b); **Langlassé** 145 (5a); **Lazor** 2316 (5a); **Leistner** 275 (5a); **Lemaire** 955 (3); **Leonard** 1614 (3), 2805 (5a), 3436 (5a), 3487 (5b), 9882 (5c), 11023 (5a), 11756 (5a), 11800 (5c), 12781 (5a), 14093 (5a), 15664 (5a); **LeSueur** 876 (5a); **Lévy** 18 (5a); **Lewis** 17365 (5a); **Liesner** 12409 (1); **Lievens** 2693 (5a); **Lillo** 72 (5c) 3835 (5a), 7633 (5b); **Liogier** 17540 (5a); **Lleras** P17083 (1); **Lloyd** s.n. (3), 1105 (5c); **López** 4024 (1); **Lorentz** s.n. (5b); **Lourteig** 350 (5b); **Loveridge** 711 (5a); **Luck** s.n. (2); **Lundell** 553 (5c), 823 (5c), 1544 (5c), 5181 (5c), 7792 (5a), 9922 (5c), 10013 (5c), 10755 (5c), 11656 (3), 12033 (5a).

Macbride 1044 (5c), 2336 (5b), 5880 (5a); **Macdonald** 1 (5b); **Mackenzie** s.n. (3), 36 (5c); **Maldonado** 535 (5a); **Malmeico** 744 (5a); **Malmierca** 744 (5c); **Maltby** 14 (5a), 220 (5a); **Maranta** 63 (5c); **Marcano** 3372 (5a); **Marshall** 2026 (2); **Martcorena** 838 (5b); **Martínez Achenbach** 2090 (5b); **Martínez Crovetto** 10005 (5b); **Martínez** s.n. (5c), 1006 (5c), 9548 (5b); **McCarthy** s.n. (5a); **McDaniel** 5173 (5a); **McDougall** 1031 (3); **McGregor** 16306 (5c); **McVaugh** 16908 (5a); **Mejía** 1044 (5a), 7137 (5a), 7780 (5a); **Mell** 2011 (5a); **Méndez Ton** 4622 (5c); **Mereles** 521 (5c), 1612 (5a), 3331 (5a), 5514 (5a); **Merrill King** 2761 (5c), 3818 (5c), 4368 (5c); **Mexia** 6068 (1); **Meyer** 146 (5c), 16284 (5b), 35481 (5a); **Miers** 85 (5b), 582 (5a), 1310 (5b); **Miller** 243 (5a); **Moldenke** 19763 (5b); **Molfino** s.n. (5c); **Moore** 334 (5a), 19345 (3); **Moraes Vasconcellos** 2916 (1); **Morong** 905 (5c), 1048 (5b); **Morrison** s.n. (3), 1155 (3); **Morrone** 2362 (5b), 3057 (5a), 4479 (5c); **Morton** 2947 (5c), 8814 (5c), 10293 (5a), 10671 (5c); **Moseley** s.n. (3); **Muensch** 22049 (3); **Múlgura** 4256 (5b); **Müller** 106 (5c).

Naranjo 804 (5b); **Nease** 518 (3); **Nee** 32690 (5c), 39457 (5c), 43901 (3), 43998 (5a), 50262 (5c); **Neill** 4042 (1); **Nelson** 40 (5c), 336 (5c), 387 (2), 2584 (5a), 6385 (5a); **Newman** 16 (5c), 46 (5c); **Nicolas** s.n. (5a); **Nicora** 656 (5b), 734 (5b), 1319 (5b), 1343 (5b), 1637 (5b), 2032 (5b), 2816 (5b), 3472 (5a), 4013 (5b), 4303 (5b), 4307 (5a), 17805 (5b); **Niglia** 15 (5b); **Norton** s.n. (3), 394 (3); **Novara** 8141 (5b), 8511 (5b); **Novelo** 1707 (5c), 1951 (5c).

Ohba 201 (5a); **Ohlendorf** s.n. (3); **Olmstead** 2004-159 (5b), 2007-65 (5a); **Orcutt** s.n. (3), 1300 (3), 2985 (5c); **Ortega** 4205 (5c), 4517 (5c), 5415 (5c); **Osten** 6385 (5b).

Palacios 351 (5c); **Palmer** 140 (3), 341 (5a), 819 (5a), 1154 (5a), 3820 (3), 6425 (5a), 10223 (5c), 34021 (5a); **Pammel** 87 (3); **Panigatti** 688 (5b); **Pappi** 4529 (5a); **Parish** 1099 (3); **Pascual Alvaro** 276 (5c); **Pastore** s.n. (5a), 208 (5b), 324 (5b); **Paull** s.n. (2); **Pedersen** 1873 (5b), 6658 (5b), 10853 (5c), 12483 (5b), 14001 (5a); **Pelosi** 5 (5b), 6 (5b), 32 (5b), 46 (5b), 56 (5b), 702 (5b); **Pennell** 3840 (1), 4675 (1), 16782 (5a), 18006 (5c); **Pensiero** 2877 (5a), 2916 (5a), 3374 (5b); **Perez Moreau** 3419 (5b); **Pfister** 9461 (5a); **Philippi** 309 (5b), 310 (5b); **Phillipson** 2262 (5a); **Pierotti** 4 (5c), 7 (5c); **Pitard** 467 (5a); **Pittier** 6345 (5a), 6493 (5c), 8782 (5c), 10187 (5c), 11031 (5a), 11722 (1), 12322 (1), 13116 (5a); **Pleyte** 1 (5a); **Pocklington** 196 (3); **Pollard** 1310 (3); **Poore** 1365 (5a); **Pope** 402 (5a); **Prance** 2593 (1), 7347 (1), 16313(1), 23934 (1); **Prey** 6 (5c); **Prichard** 1 (5b); **Prina** 3099 (5b); **Prindle** 2 (3); **Proctor** 18677 (5c); **Purpus** 6180 (3); **Puysegur** s.n. (5b).

Quentin 563 (5a); **Questel** 548 (5a), 616 (5a), 656 (5a), 663 (5a), 4570 (5a), 4680 (5a).

Ragonese 2144 (5b), 2827 (5b), 6802 (5b), 7050 (5a), 9725 (5b); **Ramirez Arango** 4597 (1); **Raulerson** 15317 (5a), 22644 (5a); **Raunkiaer** 849 (5a), 1216 (5a); **Razakamalala** 985 (5a); **Reboud** 1325 (5a); **Reverchon** 1571 (2), 3254 (2); **Richardson** s.n. (5a); **Rickering** 1276 (3); **Ricksecker** 223

(5c); **Ridway** s.n. (3); **Rimachi** 536 (1), 8311 (1), 8370 (1), 8738 (1), 11104 (1); **Rinehart** 19243 (5a); **Robertson** 214 (5a); **Robledo** 551 (1); **Rocha** 3721 (5a); **Rodin** 4156 (5a); **Rodriguez** 33 (5c), 132 (5b), 1113 (5c), 2912 (5a), 3092 (5a), 3476 (1), 3976 (5c), 4179 (5a); **Rogers** 6006 (2); **Roig** 9853 (5c); **Rojas** 1884 (1), 1886 (5c), 2523 (1), 7822 (5c), 8872 (5c); **Roldán** 1024a (5c); **Romanczuk** 10 (5b); **Romero** 968 (5a); **Romero Castañeda** 10439 (5a); **Romo** 47 (5c); **Rondeau** 247 (1); **Roos** 5306 (3); **Rosales** 2216 (1); **Rose** 4011 (5c), 4214 (5a), 10276 (5c), 13258 (5c), 13975a (5c), 14131 (5c), 14781 (5c), 18628 (5b), 24321 (5c), 24387 (5c); **Rosengurt** B 1372 (5b), B 1399 (5b); **Rotman** 741 (5b); **Rowan** 1035 (3); **Roybal** 266 (5c); **Rúgolo** 1001 (5b); **Ruiz Leal** 1138 (5b), 2172 (5b); **Runyon** 276 (5a), 440 (5a), 6076 (5a); **Rusby** 6 (1); **Rydberg** 922 (2).

Sachet 423 (5a); **Saer** 241 (5c), 827 (1); **Sagástegui** 7193 (5b); **Sanzin** 112 (5b); **Saravia Toledo** 1711 (5c); **Sargent** 11 (5a); **Saunders** 817B (3); **Scala** 47 (5b); **Scarpa** 487 (5a); **Schiller** 966 (3); **Schinini** 12285 (5b), 12619 (5b), 18015 (5c), 18081 (5c), 19062 (5b), 24205 (5a), 25762 (5a); **Schultz** 3492 (5b); **Schunke** 2791 (1); **Scolnik** 1164 (1), 1244 (5c); **Scully** 810 (3); **Seaton** s.n. (5c); **Seijo** 2432 (5b), 2582 (5b); **Semper** s.n. (5b); **Semple** 595 (2); **Sennen** 8158 (5a); **Serrano** 138 (5b); **Seymour** 5351 (1); **Shafer** 858 (5a), 1559 (1), 10623 (5a); **Shepard** 277 (5a); **Shinners** 8575 (5a), 8636 (3); **Silva** 1553 (1); **Silverstone** 867 (5c); **Simpson** 582 (1), 583 (5c); **Singer** 270 (3); **Smith** s.n. (3), 31 (5b), 614 (3), 677 (3), 704 (5a), 772 (2), 774 (2), 1166 (5a), 3124 (5c), 4130 (3); **Snyder S-121** (2); **Solís Neffa** 998 (5c); **Somes** 3345 (3), 3368 (3), 3625 (3); **Sorensen** 7116 (5c); **Sosa** s.n. (5a); **Soukup** 1844 (5c); **Souza** 6981 (5b), 7862 (5a); **Souza Novelo** 260 (5a); **Spellman** 954 (5b), 2471 (5a); **Sperry** 582 (3); **Standley** 9659 (3), 9789 (3), 14266 (5c), 20994 (5c), 23865 (1), 24637 (5c), 40452 (5c), 53825 (5a), 55007 (5c), 55685 (1), 55765 (5c); **Stanford** 1992 (5c); **Steele** s.n. (3); **Stehlé** 2301 (5c), 5909 (5c), 6179 (5c), 6941 (5c); **Steinbach** 2726 (5c), 2888 (5c), 6038 (5b); **Stephenson** s.n. (3); **Stergios** 8135 (1); **Stevens** 8026 (1), 8219 (1), 8914 (1), 8978 (1), 12428 (1), 12979 (1), 18735 (1); **Stevens** s.n. (3), 624 (2); **Stevenson** 1690 (5a); **Stewart** 3302 (5c); **Steyermark** 45930 (5c), 130972 (5c); **Stoddart** 7038 (5a), 8123 (5a); **Stofella** 4 (5b); **Stork** 8977 (5c); **Stratton** 213 (5a); **Straw** 2404 (5b); **Studhalte** 1541 (5c); **Subils** 986 (5a); **Sumithraarachchi** 779A (5a); **Svenson** 11164 (5b); **Swanson** 2419 (3); **Symon** 13087 (5b).

Täckholm s.n. (5a); **Tamayo** 1091 (5c), 1366 (5a), 3353 (5c), 3525 (1); **Taylor** 5863 (3), 12572 (5c); **Teague** 548 (5c); **Tharp** s.n. (5a), 1203 (5c); **Thieme** 5407 (5c); **Thieret** 21701 (3); **Thorne** 14644 (3); **Tolaba** 2295 (5a); **Tolstead** 411077 (2), 411082 (2), 411607 (2); **Townsend** 29 (5c); **Tracy** 7532 (3); **Troiani** 3227 (5b), 3611 (5a), 3900 (5b); **Troncoso** 82 (5b), 180 (5b), 381 (5b), 1241 (5b); **Tún Ortiz** 1260 (5c); **Turckheim** 1259 (5c); **Turner** 6041 (5c); **Tyler** 78 (5c); **Tyson** 2256 (5a).

Ulibarri 967 (5b), 994 (5a); **Umana** s.n. (5b); **Underwood** 376 (5c); **Urban** 565 (5c), 3390 (5c), 3543 (5c).

Valeur 447 (5b), 798 (5a); **Vanderbilt** 2665a (3), 2665b (3), 2665c (3), 2665d (3); **Vanni** 88 (5c), 1898 (5c), 2078 (5c); **Vasconcellos Sobinho** 4099 (1); **Vásquez** 9855 (1); **Velarde** 582 (5b); **Velez** 2242 (1); **Ventura** 7720 (5a); **Venturi** 93 (5b), 486 (5a), 2304 (5c), 2433 (5a), 3945 (5b), 4903 (5b), 5114 (5c), 5577 (5c); **Verma** 195 (5a); **Vestal** s.n. (2); **Vignati** 7020 (5b); **von Türkheim** 1259 (5c), 1373 (5c).

Waby 49 (5c); **Wagner** 3692 (2); **Wagnon** 2 (3); **Walker** 70 (5c); **Wang** 41657 (5a); **Ward** s.n. (2), s.n. (5a); **Waterfall** 1336 (3), 4361 (5c), 4685 (2), 12497 (5a); **Webber** 34 (5a); **Webster** 10731 (5a), 10745 (5a); **Wheeler** 14154 (5a), 20313

(3); **Whitefoord** 9519 (5c); **Wiesenborn** 13322 (5a); **Wiley** 509 (5a); **Wilkinson** 118 (5c); **Williams** s.n. (3), 349 (3); **L. Williams** 2475 (1), 13351 (1); **Wilson** 8296 (5a); **Witherspoon** 8777 (5a); **Wolff** 48a (5c), 48b (5c), 1099 (3), 1240 (3), 2398 (5c), 2840 (5b), 4092 (3); **Woodson** 931 (5a); **Woytkowski** 6749 (5b); **Wright** s.n. (5c), 1243 (3), 3164 (5a); **Wurdack** 41197 (1); **Wynd** 430 (5c).
Xu 1 (5b).

Yuncker 8094 (5c), 8095 (5c).
Zabala 201 (5c); **Zamora** 459 (5c), 1404 (1); **Zanoni** 16981 (5a), 39537 (5a); **Zardini** 40372 (5b), 40451 (5c), 45832 (5c), 45976 (5c), 58066 (5c); **Zhu** 1316 (3); **Zöllner** 10679 (5b), 12790 (5a), 11283 (5a); **Zuloaga** 1481 (5c), 1603 (5b), 2655 (5a), 2834 (5a), 6338 (5c).
s. coll. (5a); s. coll. 116 (5a); s. coll. 195 (5b); s. coll. 449 (5a).